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Revision of Afro-Malagasy *Otomops* (Chiroptera: Molossidae) with the description of a new Afro-Arabian species

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Abstract

The paucity of data for the molossid bat *Otomops* throughout its range has hindered our ability to resolve the number of *Otomops* species present within the Afro-Malagasy region (including the Arabian Peninsula). This paper employed an integrative approach by combining morphometric (cranial morphology) and molecular (mitochondrial cytochrome *b* and D-loop sequences, nuclear intron sequences and microsatellites) data to identify the number of *Otomops* taxa occurring in the Afro-Malagasy region. Three taxa were identified, two of which could be assigned to existing species, i.e. *O. martiensseni* and *O. madagascariensis*. The third taxon, previously recognised as *O. martiensseni* (Matschie 1897), is described herein as a new species, *Otomops harrisoni* **sp. nov.**, and can be differentiated from *O. martiensseni* s.s. based on both molecular and morphometric data. Locality data of specimens belonging to *O. harrisoni* suggest that its distribution range extends from the Arabian Peninsula through to Eritrea and south to Ethiopia and Kenya.

Key words: systematics, molecular genetics, morphometrics, ecological niche modelling, northeastern Africa

Introduction

The Palaeotropical genus *Otomops* Thomas, 1913 (Molossidae) currently includes seven recognised species (Simmons 2005; Hutcheon & Kirsch 2006). Five of these are distributed in the Oriental region, including southern India, Java, Papua New Guinea, Cambodia, the Philippines and Indonesia (Alor Island), which suggests that this genus may have an Oriental origin (Lamb *et al*. 2008). The other two species have a wide but somewhat sparse distribution throughout the Afro-Malagasy region, including the Arabian Peninsula (Peterson *et al*. 1995; Simmons 2005). *Otomops martiensseni* (Matschie 1897) is known from Yemen on the Arabian Peninsula (Al-Jumaily 1999) and the African mainland from South Africa in the south, to Ethiopia and Eritrea in the northeast (Kock & Zinner 2004) and Ivory Coast to the west (Lamb *et al*. 2008). *Otomops madagascariensis* Dorst, 1953 mostly occurs on the drier, western parts of Madagascar (Goodman & Raherilalao 2014).

Otomops martiensseni and *O. madagascariensis* are considered to be separate species (Simmons 2005; Lamb *et al*. 2008) although *O. madagascariensis* was formerly classified as a subspecies of *O. martiensseni* (Long 1995). Historically, there has also been debate regarding the existence of *O. icarus* Chubb 1917 (Meester *et al*. 1986; Simmons 2005). *Otomops martiensseni* is the only mainland African species, although *O. icarus* (Durban, South Africa) was once considered a species, subspecies or synonym of *O. martiensseni* (Chubb 1917; Long 1995; Mickleburgh *et al*. 2008). Lamb *et al*. (2006) showed that populations from east Africa and South Africa are distinct but have low divergences in mitochondrial cytochrome *b* (2.50%) and D-loop sequences. Nuclear data (PCR-RAPDs), however, revealed an opposing result with high genetic similarities between east African and South African individuals (Lamb *et al*. 2006). Fenton *et al*. (2002) reported morphological differences between

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specimens from Madagascar and/or Durban versus those from east Africa, the latter appearing significantly larger. Peterson *et al*. (1995) used multivariate analyses of craniodental and external characters to support Dorst's (1953) view that *O. madagascariensis* is a distinct species. The above morphological and genetic analyses suggest that there are two or perhaps three species within this species group.

More recently Lamb *et al*. (2008) identified three reciprocally-monophyletic cytochrome *b* and D-loop clades of Afro-Malagasy *Otomops*: *O. madagascariensis*, *O. martiensseni* from eastern and northeast Africa (Ethiopia, Kenya and Yemen) and *O. martiensseni* from southern (Burundi, South Africa, Tanzania and Zimbabwe) and western (Ivory Coast) Africa. The morphometric data of Richards *et al*. (2012) also supports the recognition of the above three Afro-Malagasy *Otomops* lineages, and includes additional *O. martiensseni* samples from previously unsampled regions of eastern, western and southern Africa. The aim of this study was to resolve the taxonomic status of these three clades by analysing an expanded dataset of mitochondrial and nuclear DNA markers, as well as cranial morphology.

Material and methods

Sampling. Material for both molecular and morphological datasets was obtained from 15 museums, including associated acronyms, and sampling of individuals from extant roost colonies (Appendix 1). Samples for DNA analyses were stored in lysis buffer or 90% ethanol and comprised heart, lung, liver, kidney and/or thoracic muscle tissue. Wing punches of individuals from Durban, South Africa, were collected under Ezemvelo KZN Wildlife and 'ToPS' permit numbers OP 853/2009 and OP 360/2013. Figure 1 illustrates the areas of the Afro-Malagasy region that were sampled.

Molecular data. *Mitochondrial cytochrome* b *and D-loop*. The methods used for obtaining DNA sequence data from the mitochondrial cytochrome *b* and D-loop regions are presented in Lamb *et al*. (2008) and include DNA isolation, PCR amplification of both regions and DNA sequencing protocols. Due to the relatively smaller sample size (n = 60) used in Lamb *et al*. (2008), the molecular dataset was expanded (n = 106) to include additional samples from across the Afro-Malagasy region (Appendix 1). Mitochondrial cytochrome *b* and D-loop sequences were placed into a concatenated dataset comprising 1322 nucleotides and jModelTest v.0.1.1 (Guindon & Gascuel 2003; Posada 2008) was applied using the Akaike Information Criterion (AIC) to determine the most appropriate model of evolution (GTR+I+G) for use in Bayesian analyses. Relative genetic p-distances between and within the groups were calculated in PAUP* v.4.0b10 (Swofford 2002). The dataset was analysed using maximum parsimony in PAUP* v.4.0b10 and Bayesian Inference as implemented in MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001). Samples from Tanzania and Zimbabwe were analysed on the basis of cytochrome *b* data only (1012 nucleotides) as we were unable to amplify the D-loop region of these samples; their relative positions have however been included in the resulting tree. For maximum parsimony analysis starting trees were obtained by stepwise addition. The tree-bisection-reconnection branch-swapping algorithm was used with a random addition sequence in which 1 tree was held at each step, with 10 replicates. One thousand bootstrap replicates were carried out using a heuristic search. Bayesian analyses were run using four Markov chains for 5 million generations each, sampling every 100 generations, ensuring that the standard deviation of the split frequencies was less than 0.01. The chains were heated with the temperature scaling factor T = 0.02. The first 50,000 trees were discarded as burn-in, in each case having checked in a preliminary run that this was more than sufficient to achieve stationarity. A 50% majority-rule consensus tree was constructed from the remaining trees.

Nuclear intron sequence data. Genomic DNA was isolated from 7 molossid species (n = 9), *Otomops martiensseni* s.s., *O. harrisoni* **sp. nov.**, *O. madagascariensis*, *Mops leucostigma*, *M. condylurus*, *Mormopterus francoismoutoui* and *M. jugularis*, using the DNeasy® DNA isolation kit (QIAGEN). A total of 5 nuclear introns were PCR amplified: feline sarcoma proto-oncogene (FES), growth hormone receptor (GHR), rhodopsin (RHO1) (Venta *et al*. 1996), protein-kinase C1 (PRKC1) (Matthee *et al*. 2001) and pyridoxine 5'- phosphate oxidase intron 3 (PNPO-Intron 3) (Igea *et al*. 2010). The optimised PCR amplifications were performed in 25 µl reactions containing 30-60 ng template DNA, 0.8 µl sterile water, 2.5 µl 10 X reaction buffer (Super-Therm), 4 µl 25 mM $MgCl_2$ (Super-Therm), 0.5 µl 10 mM deoxynucleoside-triphosphate mixture (dNTPs) (Fermentas), 0.2 µl 5 U/µl *Taq* polymerase (Super-Therm) and 4 µl of 6 µM primer dilution (forward and reverse) per reaction (primer sequences available from Venta *et al*. 1996, Matthee *et al*. 2001 and Igea *et al*. 2010). The thermal cycling parameters used were as follows: 95 °C for 5 min; followed by 39 cycles of (95 °C for 30 s, primer-specific

annealing temperature for 30 s and 72 °C for 2 min); followed by 72 °C for 10 min. Primer-specific annealing temperatures were as follows: FES: 58 °C; GHR: 60 °C; RHO1: 55 °C; PRKC1: 55 °C; PNPO-Intron 3: 55 °C. Sequencing was performed on an ABI 3500 Genetic Analyzer (Applied Biosystems) at Inqaba Biotec, Pretoria, South Africa. Nuclear intron data from all 5 markers were placed into a concatenated data set comprising 2216 nucleotides. The dataset was then analysed using TCS v.1.21 (Clement *et al*. 2000) to create a statistical parsimony network at a 95% confidence (20 step connection limit) to illustrate possible connections between samples.

Nuclear microsatellite repeats. Methods used for the amplification of nuclear microsatellite repeats are presented in Ralph & Lamb (2013), detailing the optimal annealing temperatures, amplification reagents, primers and thermal cycling parameters for each of the six loci used. Every individual (n = 71) was genotyped separately to avoid any complications incurred by multiplex reactions. Patterns of genetic clustering among individuals were assessed using STRUCTURE v.2.3.4 (Pritchard *et al*. 2000), where six runs for each *K* were implemented ranging from the minimum to maximum number of sites per lineage, i.e. 1 to 6. Clustering patterns were investigated to determine the number of populations, assign individuals to these groups and to determine whether the groupings observed corresponded to geographic locality. FSTAT v.2.9.3.2 (Goudet 2002) was used to calculate the expected (H_E) heterozygosities for loci within each population.

Morphology. *Topotypic material*. Data and multivariate analyses presented in the current study are derived from Richards *et al*. (2012) and further investigations that include topotypic material of Indo-Australasian *Otomops*. We extended the previous study to include six of the seven currently recognised *Otomops* taxa: *O*. cf. *formosus* (Indonesia), *O. papuensis* (southeast Papua New Guinea), *O. secundus* (northeast Papua New Guinea), *O. wroughtoni* (India and Cambodia), *O. madagascariensis* (Madagascar) and *O. martiensseni* (Africa and Arabian Peninsula). We were unable to examine individuals of the seventh species *O. johnstonei*; where possible, we have included published morphological data on this species for comparative purposes. Specimens of *O. martiensseni* were sampled from several African countries: Burundi, Central African Republic, Ivory Coast, Democratic Republic of Congo, Djibouti, Ethiopia, Kenya, Malawi, South Africa, Tanzania, Uganda, Zambia, Zimbabwe and Yemen. Holotypes and paratypes examined in this study (n = 11): *O. madagascariensis*, type locality south of Soalala, Namoroka, Réserve naturelle intégrale no. 8, Madagascar, (MNHN 1953-1590); *O. martiensseni*, type locality Magrotto plantation, southeast Usambara Mountains, Tanzania (MNHU 97523); *O. secundus*, type locality Tapu, Madang Province, Papua New Guinea (BMNH 50.979-50.982); *O. wroughtoni*, type locality Barapede Cave, near Talewadi, South India (BMNH 12.11.24.1, BMNH 13.4.9.1-13.4.9.2, BMNH 13.4.9.4-13.4.9.6).

Craniodental morphometrics. Specimens were aged based on the degree of cusp degradation of maxillary molars, as well as skull size and shape (see Richards *et al*. 2012). Six age-classes were identified. Only adults assigned to age classes 4–6 were included in the study. Because Afro-Malagasy *Otomops* display significant heterogeneity in sexual dimorphism in cranial size and shape (Richards *et al*. 2012; Richards unpublished data), the sexes were segregated in analyses. Three morphometric data sets (craniodental measurements, dorsal and ventral landmark data) were recorded from *Otomops* crania. Analyses of these data sets produced consistent results, thus only the results of analyses of craniodental measurements, dorsal landmark data of males and ventral landmark data of females are presented herein.

Nine cranial and three dental measurements, defined in Richards *et al*. (2012), were recorded from 182 *Otomops* spp. specimens (n = 89 males, n = 93 females) by LRR using Mitutoyo callipers to 0.01 mm accuracy. The cranial measurements included: greatest skull length (GSL), braincase height (BCH), braincase breadth (BCB), mastoid breadth (MB), zygomatic breadth (ZB), inter-orbital width (IOW), palatal length (PL), tympanic bulla length (TBL), and moment arm of temporalis (MAT). The dental measurements included: maxillary toothrow length (MTR), maxillary inter-canine width (C^1C^1), and mandibular toothrow length (LTR). Principal components analyses (PCA) were performed on variance-covariance matrices of $\log_{10}$-transformed craniodental measurements of males and females, using IBM SPSS Statistics v.21 (IBM Corp. 2012) to explore patterns of morphological variation in the six Afro-Malagasy and Indo-Australasian taxa examined in this study.

Digital images of the dorsal (n = 102 males, n = 92 females) and ventral (n = 87 males, n = 91 females) views of *Otomops* spp. skulls were captured using a Fujifilm FINEPIX S8100 digital camera (Fujifilm Corporation, Japan) mounted on a tripod (x18 optical zoom, 5 megapixel resolution, 25 mm focal length, macro function). Fourteen dorsal and 16 ventral landmarks (see Richards *et al*. 2012) were captured in two dimensions from cranial images using the software program tpsDig, v.2.15 (Rohlf 2010a). Landmarks were only recorded from the left half of dorsal views and right half of ventral views of crania to avoid the effects of bilateral asymmetry. Analyses of

dorsal and ventral data sets showed minimal error levels with respect to image capture and landmark placement (data not shown). The programme tpsRelw, v.1.45 (Rohlf 2010b) was used to conduct a Generalized Procrustes Analysis (GPA) of landmark data sets. Landmark configurations of each individual were translated, rotated, scaled and superimposed to derive a consensus configuration of all specimens analysed. The GPA residuals variation was then decomposed into affine (*U*1 and *U*2) and non-affine (partial warp scores) components of shape change. Patterns of interspecific shape variation amongst Afro-Malagasy and Indo-Australasian individuals were investigated by PCA of the total shape matrix (U + W) for dorsal and ventral data sets of males and females using MorphoJ software (Klingenberg 2011). Thin plate splines that depict morphological shape changes were generated using tpsRelw (Rohlf 2010b).

Ecological niche modelling. The MaxEnt algorithm v.2.3 (Phillips *et al*. 2006) was used to predict the potential geographic ranges of two groups of Afro-Arabian *Otomops* spp. throughout sub-Saharan, central and western Africa as well as the Arabian Peninsula. The predicted environmental limits allow for the inference and comparison of the potential distribution of each group. Input data included the georeferenced distribution records (recorded to 0.001 decimal degrees) of Afro-Arabian *Otomops* (n = 30 records south/east/central/west OTU; n = 18 records northeast OTU) obtained from museum and literature records (dataset available from TMCR). Nine continuous environmental variables (WORLDCLIM database v.1.4, Hijmans *et al*. 2005) were used as predictor variables in the model, including: ALT1 (altitude); BIO1 (annual mean temperature); BIO4 (temperature seasonality); BIO5 (maximum temperature of warmest month); BIO6 (minimum temperature of coldest month); BIO12 (annual precipitation); BIO13 (precipitation of wettest month); BIO14 (precipitation of driest month) and BIO15 (precipitation seasonality). Variables were uncorrelated with a maximum value of 0.76. Bioclimatic data (grid files) were sampled at a spatial grid resolution of 2.5 arc minutes (approximately 5 km). Spatial grids of the bioclimatic variables were converted to ASC files using ArcMap v.9.3. Models were run separately with all distribution records for each respective species, a regularisation multiplier of 1.0, a maximum number of 1000 iterations and 5 replicates. Other MaxEnt settings were set to the default and the relative and absolute contribution of each bioclimatic variable to the model was assessed using the jackknife procedure in MaxEnt.

Results

Molecular analyses. *Mitochondrial cytochrome* b *and D-loop*. A concatenated data set comprising 1322 nucleotides of cytochrome *b* and D-loop data was analysed under the phylogenetic species concept using Bayesian and maximum parsimony methods; 15.20% of the sites were variable and 12.60% were parsimony informative. As both analyses produced largely congruent trees, we present a single tree showing nodal support values derived from both methods (Fig. 2). All *Otomops* spp. samples formed a strongly supported monophyletic clade (bootstrap support: 100%; posterior probability: 1.00) relative to the outgroups. The SECW (southeast, central and west African) clade comprises samples from Burundi, Ivory Coast, South Africa, Tanzania and Zimbabwe; the NEA (northeast African) clade comprises individuals from Ethiopia, Kenya and Yemen, whereas the MAD (Malagasy) clade comprises specimens from Madagascar. The position of the outgroups relative to the ingroups was also congruent across both resulting trees. Major clades within the tree were well-resolved and well-supported (clades A to G) (Fig. 2). Afro-Malagasy *Otomops* samples (clade C) divide into 2 reciprocally monophyletic clades (clades D and G) where clade G, comprising 17 haplotypes (19 samples) from Madagascar, and clade D, containing 54 African and Arabian haplotypes (87 samples), are separated by an average genetic p-distance of 3.30%. Clade D further subdivides into 2 reciprocally monophyletic sister lineages (subclades E and F) and are separated by a genetic p-distance of 2.10%. There is stronger support for the existence of discrete groups from SECW (subclade E; bootstrap support: 100%; posterior probability: 1.00) and NEA (subclade F; bootstrap support: 100%; posterior probability: 1.00) than there is for the existence of their combination into the currently-circumscribed *O. martiensseni* from mainland Africa and Yemen (clade D; bootstrap support: 90%; posterior probability: 0.88). This suggests that the subclades E and F are stronger groups than is clade D and supports their status as separate species. The mean p-distances within groups were also low within subclades E (0.70%) and F (0.30%) and within the Madagascar clade (G; 0.60%). By comparison, the mean within group p-distance for clade D was much larger (1.60%) than the distances within subclades E and F.

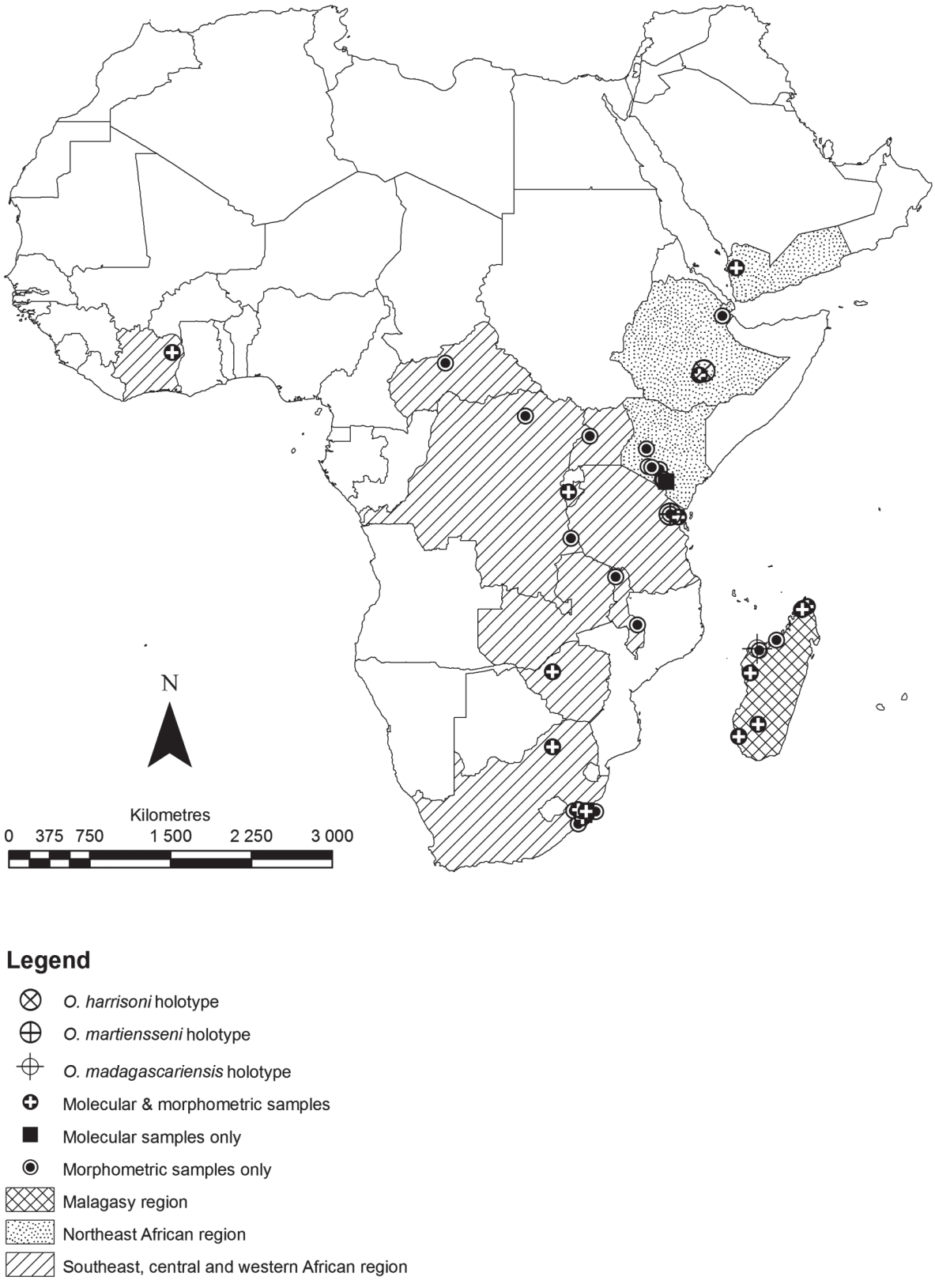

FIGURE 1. Map of the Afro-Malagasy region (including the Arabian Peninsula) depicting sampling regions and localities for specimens used for morphological and molecular analyses in this study and localities for holotype specimens.

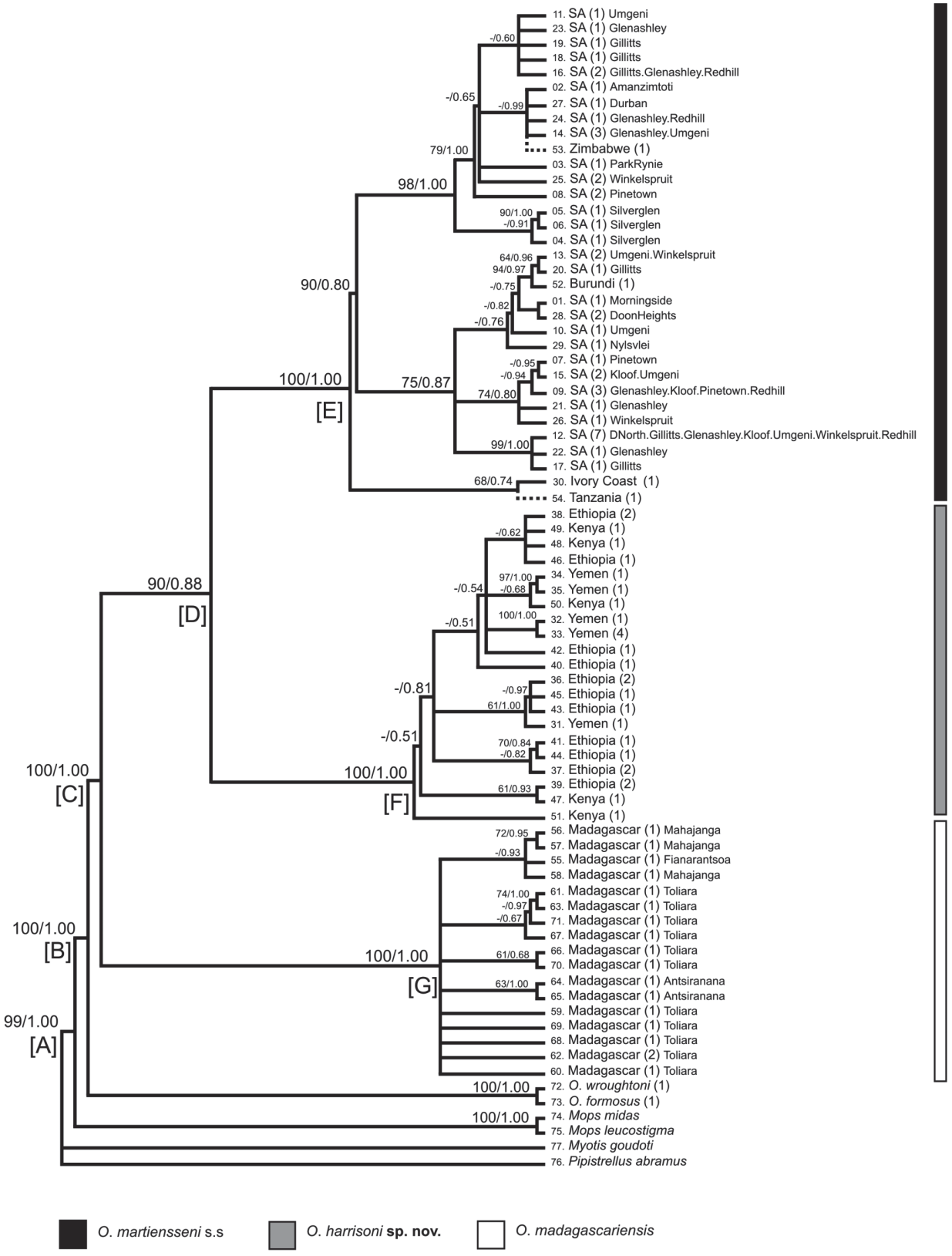

FIGURE 2. Tree based on maximum parsimony and Bayesian analyses of 1322 nucleotides of the concatenated mitochondrial cytochrome *b* gene and D-loop region sequences, depicting the relationship between 71 haplotypes of Afro-Malagasy *Otomops* species with respect to outgroups *O. wroughtoni*, *O. formosus*, *Mops midas*, *M. leucostigma*, *Pipistrellus abramus* and *Myotis goudoti* (haplotypes 72–77) (Appendix 1). Bootstrap and posterior probability support is given at the nodes according to parsimony (beginning) and Bayesian (end) analyses and dotted lines indicate relative positions of samples based on 1012 nucleotides of cytochrome *b* data only. SA = South Africa.

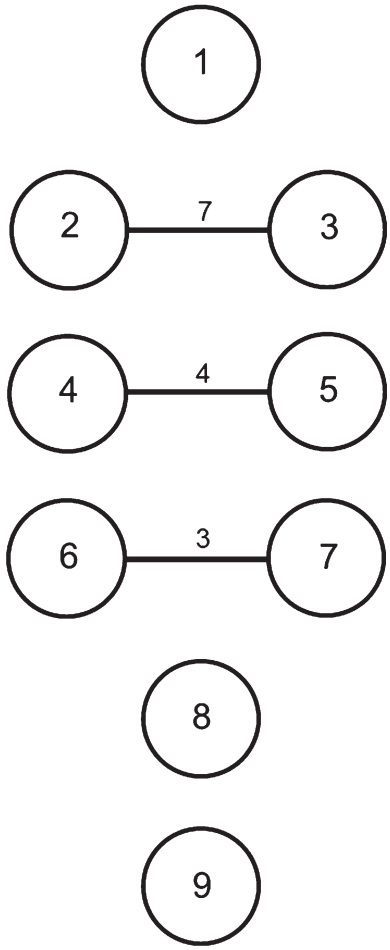

FIGURE 3. Six statistical parsimony networks formed at the 95% confidence level in an analysis of Afro-Malagasy region molossids based on 2216 nucleotides of 5 concatenated nuclear regions (FES, GHR, RHO1, PRKC1, PNPO-Intron 3). Numbers next to connection branches indicate the number of mutational steps between samples and solid lines indicate connection and confidence level. Numbers correspond to samples as follows: 1—*Otomops martiensseni* s.s. (South Africa), 2—*O. harrisoni* **sp. nov.** (Ethiopia), 3—*O. harrisoni* **sp. nov.** (Kenya), 4—*O. madagascariensis* (Madagascar), 5—*O. madagascariensis* (Madagascar), 6—*Mops leucostigma* (Madagascar), 7—*M. condylurus* (South Africa), 8—*Mormopterus francoismoutoui* (La Réunion) and 9—*M. jugularis* (Madagascar). Sample details are indicated in Appendix 1.

FIGURE 4. Graph illustrating probabilities of assignment of individuals to different genetic clusters (*Q*), where the number of clusters (*K*) = 3. Each column corresponds to an individual and each colour within the column corresponds to the relative likelihoods of that individual belonging to each of the 3 defined clusters. Numbers on the x-axis correspond to geographical areas: 1 = eastern region of South Africa (n = 43), 2 = northeast Africa (n = 20) and 3 = Madagascar (n = 8).

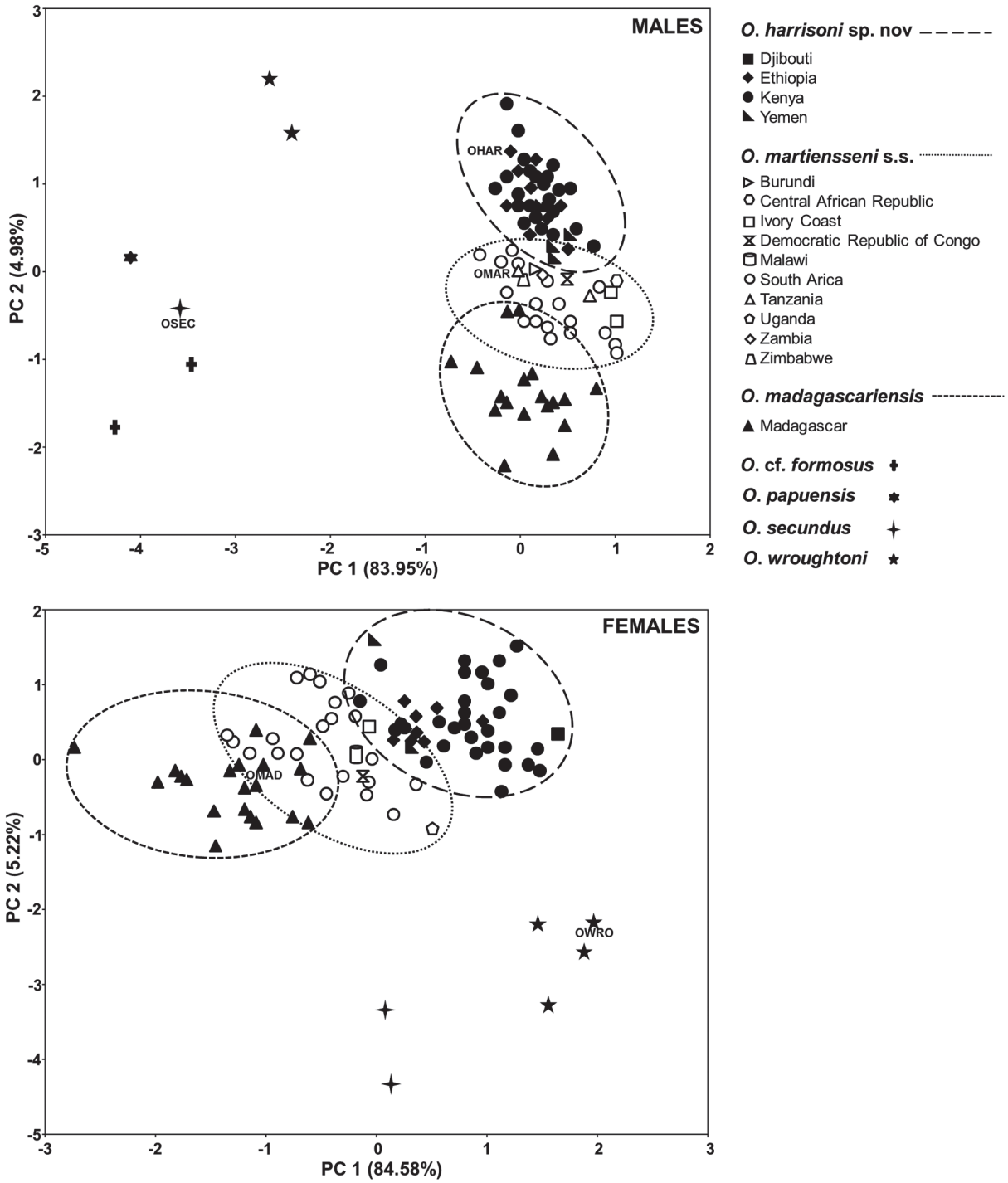

FIGURE 5. Biplot showing the first two components of principal component analyses of log–transformed craniodental variables of male and female *Otomops*. Holotypes: OHAR-*O. harrisoni* **sp. nov.**, OMAD-*O. madagascariensis*, OMAR-*O. martiensseni*, OSEC-*O. secundus*, OWRO-*O. wroughtoni*.

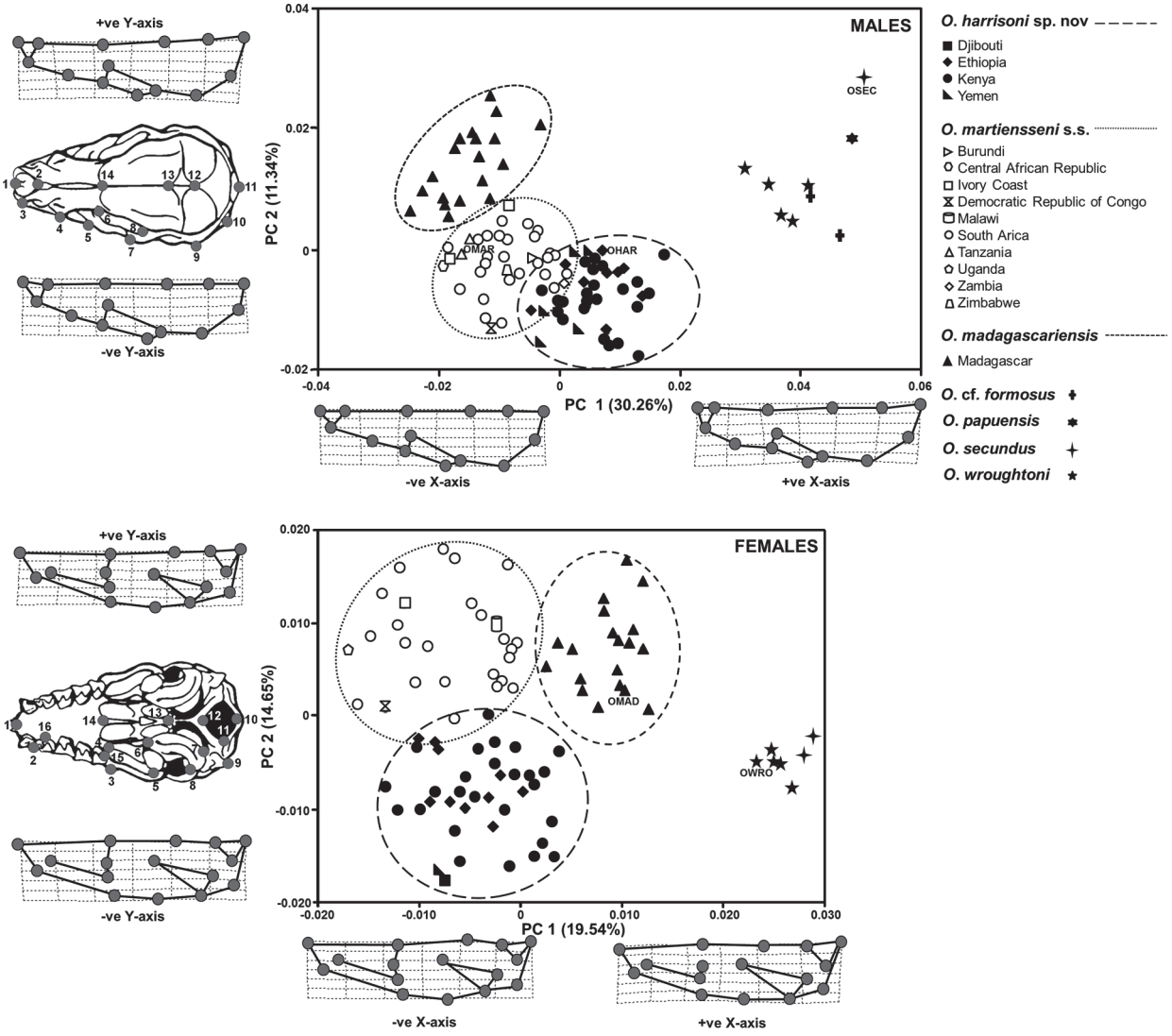

FIGURE 6. Biplot of the first two components of a principal component analysis of dorsal landmark data for males and ventral landmark data for females. Holotypes: OHAR-*O. harrisoni* **sp. nov.**, OMAD-*O. madagascariensis*, OMAR-*O. martiensseni*, OSEC-*O. secundus*, OWRO-*O. wroughtoni*. The thin plate splines depict deformations at the relevant skull landmarks (3x exaggerated).

Assuming the existence of two species, from SECW and NEA respectively, one would need to retain the name *O. martiensseni* and the other would receive a new name. The holotype of *O. martiensseni*, from Magrotto plantation in Tanzania, is included in the SECW clade based on morphometric analyses (Figs. 5–6). It was not possible to obtain DNA sequence data from the holotype, however the other experimental sample from Tanzania was also included in the SECW clade based on both morphometric and cytochrome *b* sequence (bootstrap support: 100%; posterior probability: 1.00) data (Figs. 2, 5–6). Additionally, genetic distances support this finding: p-distances between Tanzania and the remainder of the SECW clade and the NEA clade are 0.50% and 2.50%, respectively, indicating that the Tanzanian specimen used shows a closer association to the SECW clade. Based on this we propose that the members of the SECW clade retain the name *O. martiensseni*. Samples from the NEA subclade (F) would therefore constitute a new species: *O. harrisoni*, described herein. This currently comprises samples from Ethiopia, Kenya and Yemen, including the designated holotype HZM 60.36217 from Ethiopia (haplotype number 42). Studies based on more extensive samples would be needed to clarify whether there is any overlap in the distributional ranges of *O. martiensseni* s.s. and *O. harrisoni* especially in the area surrounding the

Kenya/ Tanzania border where the current ranges of the two clades abut. There is little to no structuring based on geographical locality within each of the major clades. Indo-Australasian *Otomops* representatives, *O. wroughtoni* and *O. formosus*, appear sister to the Afro-Malagasy species. *Otomops formosus* and *O. wroughtoni* were each separated by similar p-distances (10.20% and 9.60%, respectively) from each of the three Afro-Malagasy *Otomops* clades and *O. formosus* and *O. wroughtoni* were separated by a p-distance of 6.20%.

Nuclear intron sequence data. In the concatenated data set of 2216 nucleotides from 5 nuclear introns (FES, GHR, RHO1, PRKC1 and PNPO-Intron 3), 17.80% of the sites were variable and 10.00% were parsimony informative. Sequences were analysed using parsimony to create a statistical network (Fig. 3). When analysed at a 95% connection limit, 6 separate networks were formed, corresponding to: *O. harrisoni* (samples 2 and 3); *O. martiensseni* s.s. (sample 1); *O. madagascariensis* (samples 4 and 5); *Mops leucostigma*/*M. condylurus* (samples 6 and 7); *Mormopterus francoismoutoui* (sample 8); and *M. jugularis* (sample 9). The closely related *Mops condylurus* and *M. leucostigma* form a single network, but this is expected given that cytochrome *b* data analysis shows strong support for a monophyletic *Mops* clade, including *M. leucostigma*, *M. condylurus* and *M. midas* (Ratrimomanarivo *et al*. 2008).

Nuclear microsatellite repeats. STRUCTURE analysis clearly reveals genetic structure at a regional level (SECW, NEA, MAD), where the model $K = 3$ best fits the data (Fig. 4). Identical clustering patterns with similar cluster membership (Q) values were created for each $K = 3$ run. Local population structure appeared weak; clusters based on geographical location of collection sites could not be identified and individuals were inter-mixed across the various localities within each region. Dispersal movements across the three regions were not detected as all individuals were assigned to the region from which they were sampled. Nuclear microsatellite data analysed in STRUCTURE assignment tests showed high level gene flow among samples within the same regions (SECW, NEA, MAD), irrespective of distance between localities; maximum distances between colonies in SECW and NEA regions are ~37 km and 2250 km, respectively. Evidence of high gene flow, indicative of a random mating structure among individuals (Bogdanowicz *et al*. 2012), was also provided by the moderate to high expected heterozygosity (H_E) statistics within each of the Afro-Malagasy *Otomops* groupings: SECW = 0.7, NEA = 0.6 and MAD = 0.5.

Morphology. *Craniodental morphometrics*. In general, *Otomops harrisoni* is the largest taxon within the genus, both in overall body size (Table 1) and in cranial size (Table 2). The first three components from PCA of craniodental measurements explained 93.78% of morphological variation in males and 93.51% in females (Table 3). Males from the Afro-Malagasy region separated along PC2, as did those from the Indo-Australasian region, whereas females from the two biogeographic regions separated along PC1 (Fig. 5). Afro-Malagasy males separated from Indo-Australasian males along PC1, whereas the females from those regions separated along PC2. Palatal length (PL) and maxillary toothrow (MTR) loaded the highest on PC2 for females (Table 3), indicating that separation of African from Asian females was largely attributed to morphological changes localised within the palatal and rostral region. Afro-Malagasy males separated along PC2 into three distinguishable taxa representing *O. madagascariensis*, *O. martiensseni* s.s. and *O. harrisoni* (Fig. 5). Afro-Malagasy females separated according to size into three slightly overlapping groups, along PC1 (Fig. 5). Based on factor loadings presented in Table 3, male and female *O. harrisoni* were distinguished from other African individuals by greater inter-orbital width and proportionately wider braincases and greater braincase height (excl. tympanic bullae).

Principal component scatter plots based on landmark data for male and female *Otomops* show that Indo-Australasian *Otomops* were well separated from Afro-Malagasy individuals (Fig. 6). Indo-Australasian species were, in general, characterised by short nasals that were laterally flared, short yet broad rostra, broad occipital ridges, pointed supraoccipitals and long, wide braincases. As with craniodental measurements, dorsal landmark data indicated three morphologically identifiable Afro-Malagasy taxa (Fig. 6). Compared to Indo-Australasian *Otomops*, crania of African taxa were characterised by proportionately longer rostra, and round and shorter braincases. The crania of *O. harrisoni* were characterised by proportionately broader rostra, a less angular braincase (with reference to the mastoid region), larger nasals, and broader, longer bullae relative to *O. martiensseni* s.s. and *O. madagascariensis*.

TABLE 1. External measurements (mm) and mass (g) of Afro-Malagasy and Indo-Australasian *Otomops* species including *Otomops harrisoni* **sp. nov.** Mean, standard deviation, range and sample size (n) are provided. Measurements for all specimens, including those of the referred specimens are based on museum specimen records and published data. Hindfoot length is generally reported without the claw, unless otherwise stated.

Taxon	Total length	Tail length	Hindfoot length	Ear length	Forearm length	Body mass
O. harrisoni **sp. nov.** (males)						
Holotype HZM 60.36217[1]	151.2	47.3	14.5	38	72.8	–
Paratypes included in this study[1]	148.2 ± 4.55	48.4 ± 5.45	13.0 ± 0.26	35.9 ± 0.49	69.5 ± 1.42	–
	143.2–152.1, n=3	43.0–53.9, n=3	12.7–13.1, n=3	35.3–36.2, n=3	68.4–71.1, n=3	
Other referred specimens	151.1 ± 5.48	49.6 ± 2.92	13.2 ± 1.27	39.8 ± 2.37	70.7 ± 1.92	38. 8 ± 3.75
	139.5–163.0, n=33	42.6 –54.0, n=33	11.0–16.0, n=33	35.9–46.0, n=33	63.8–74.0, n=37	31.5–45.0, n=31
O. harrisoni **sp. nov.** (females)						
Paratypes included in this study[1]	139.5 ± 5.15	47.2 ± 3.48	13.4 ± 1.23	35.9 ± 1.44	69.1 ± 1.26	-
	130.0–145.0, n=10	40.0–53.1, n=10	12.0–16.1, n=10	33.6–36.8, n=10	67.2–70.8, n=10	
Other referred specimens[1]	151.1 ± 5.25	49.0 ± 4.48	13.0 ± 1.00	38.1 ± 1.94	69.5 ± 1.63	39.2 ± 4.77
	138.0–158.0, n=27	40.0–58.0, n=28	11.27–15, n=28	34.0–41.0, n=28	65.7–72.7, n=28	26.8–45.0, n=24
O. martiensseni (males)						
Holotype MNHU 97523[2]	–	43	–	37	66	–
Other specimens[1]	140.9 ± 8.50	44.4 ± 4.11	11.6 ± 1.12	37.6 ± 3.5	65.8 ± 1.60	31.3 ± 4.17
	130.0–155.0, n=15	39.0–52.0, n=17	10.0–14.0, n=16	32.0–42.0, n=14	60.5–68.0, n=23	25.0 –38.0, n=6
O. martiensseni (females)						
Adult specimens[1]	136.4 ± 6.41	43.2 ± 2.44	10.9 ± 1.25	34.6 ± 3.72	63.5 ± 1.53	28.2 ± 2.31
	127.0–148, n=18	40.0–49.0, n=18	9.0 -13.0, n=19	29.0–41.0, n=20	60.0–66.3, n=22	25.0–32.0, n=9
O. madagascariensis (males)						
Adult specimens[1]	139.3 ± 3.82	43.8 ± 3.27	9.8 ± 0.79	40.2 ± 1.32	63.2 ± 1.32	26.2 ± 1.94
	132–146, n=20	38–50, n=20	8.0–11.0, n=20	36.0–42.0, n=20	60.0–66.0, n=20	22.0–28.0, n=20
O. madagascariensis (females)						
Holotype MNHN 1985-1590[3]	128.3	44.5	–	31.3	62.6	–
Other specimens[1]	133.4 ± 4.47	41.3 ± 4.01	9.4 ± 0.63	37.3 ± 1.84	61.1 ± 1.31	24.2 ± 2.07
	126.0–142.0, n=16	34.0–49.0, n=16	9.0–13.0, n=16	33.0–41.0, n=16	60.0–64.0, n=16	19.5–25.5, n=16
O. wroughtoni (males)						
Other specimens including paratypes included in this study[1,4]	136.5 ± 4.88	44.2 ± 4.41	12.2 ± 1.38	32.7 ± 1.34	66.1 ± 0.64	–
	127.9–142.0, n=6	36.1–49.0, n=5	10.4–14.0, n=6	31.5–34.8, n=6	65.6–66.5	

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TABLE 1. (Continued)

Taxon	Total length	Tail length	Hindfoot length	Ear length	Forearm length	Body mass
O. wroughtoni (females)						
Holotype BM 12.11.24.1[4]	145	46	10.0	33	68	–
Other specimens including paratypes represented in this study[1,4]	131.0 ± 4.11	41.5 ± 4.16	11.7 ± 1.35	33.1 ± 1.35	66.1, ± 0.64	–
	127.9–137.0, n=4	36.1–46.0, n=4	10.4–13.5, n=4	31.5–34.8, n=4	65.5–66.5, n=2	
O. papuensis (male)						
Adult specimen (BMNH 73.136)[5]	–	–	–	–	49.6	–
O. papuensis (females)						
Holotype MCZ 45769[6]	97	30	10.6*	22.2	49.2	–
Adult specimen (BMNH 73.137)[5]	–	–	–	–	50.2	–
O. formosus (males)						
Holotype RMNH 15322[7, 8]	–	43	–	30	59.7	–
Other specimens[1]	120 ± 7.07	37.5 ± 2.12	10.5 ± 0.71	29.5 ± 0.71	59.0 ± 0	26.5 ± 0.71
	115–125, n=2	36.0–39.0, n=2	10.0–11.0, n=2	29.0–30.0, n=2	n=2	26.0–27.0, n=2
O. formosus (female)						
Paratype[8]	–	–	–	–	57.4	–
O. johnstonei (male only, no data available for females)						
Holotype M 37986[8]	123.1	43.7	11.9	31.1	60	19.5
O. secundus (male)						
Holotype BM 50.982[9]	108	37	10	24	58	–
O. secundus (females)						
Paratypes included in this study[9]	106.0 ± 0	37.0 ± 1.41	10.0 ± 0	24.6 ± 0.42	57.5 ± 0.71	–
	n=2	36.0–38.0, n=2	n=2	24.0–24.3, n=2	57.0–58.0, n=2	

[1] Taken from collectors notes and/or museum records; [2] Matschie (1897); [3] Dorst (1953); [4] Thomas (1913); [5] Hill (1983); [6] Lawrence (1948); [7] Chasen (1939); [8] Kitchener *et al.* (1992); [9] Hayman (1952). *With claw (c.u.)

TABLE 2. Craniodental measurements (mm) of Afro-Malagasy and Indo-Australasian *Otomops* species including *Otomops harrisoni* **sp. nov.** Mean, standard deviation, range and sample size (n) are provided. GSL = greatest skull length, BCH = braincase height, MB = mastoid breadth, ZB = zygomatic breadth, IOW = inter-orbital width, BCB = braincase breadth, PL = palatal length, MTR = maxillary toothrow length, UCW = maxillary inter-canine width, LTR = mandibular toothrow length, MAT = moment arm of temporalis and TBL = tympanic bulla length. Measurements taken by LRR, including those provided from published data in the literature, unless otherwise stated.

Taxon	GSL	BCH	MB	ZB	IOW	BCB
O. harrisoni **sp. nov.** (males)						
Holotype HZM 60.36217	28.6	9.5	14.3	14.9	6.7	11.7
Paratypes	27.9 ± 0.15	9.2 ± 0.28	13.6 ± 0.05	14.1 ± 0.12	6.2 ± 0.22	11.7 ± 0.18
	27.75–28.05, n=3	8.97–9.51, n=3	13.59–13.69, n=3	13.98–14.21, n=3	5.97–6.40, n=3	11.50–11.85, n=3
Other referred specimens	28.5 ± 0.33	9.4 ± 0.17	14.0 ± 0.16	14.5 ± 0.20	6.5 ± 0.18	11.6 ± 0.22
	28.03–29.26, n=34	9.08–9.82, n=34	13.52–14.34, n=34	14.10–14.89, n=34	6.13–6.74, n=34	11.17–12.05, n=34
O. harrisoni **sp. nov.** (females)						
Paratypes	26.6 ± 0.23	9.1 ± 0.14	13.3 ± 0.12	13.7 ± 0.15	6.1 ± 0.11	11.3 ± 0.12
	26.36–27.02, n=9	8.89–9.40, n=9	13.19–13.55, n=9	13.48–14.04, n=9	5.95–6.26, n=9	11.06–11.38, n=9
Other referred specimens	27.1 ± 0.35	9.1 ± 0.18	13.5 ± 0.16	13.9 ± 0.22	6.3 ± 0.13	11.4 ± 0.21
	26.23–27.92, n=32	8.70–9.46, n=32	13.05–13.83, n=32	13.38–14.30, n=32	5.93–6.58, n=32	10.96–11.98, n=32
O. martiensseni (males)						
Holotype MNHU 97523	27.2	8.4	13.6	14.2	6.4	11.5
Other specimens	27.5 ± 0.69	8.6 ± 0.24	13.3 ± 0.42	14.0 ± 0.33	6.2 ± 0.22	11.1 ± 043
	26.52–28.78, n=27	8.21–9.01, n=27	12.13–13.78, n=27	13.39–14.43, n=27	5.73–6.47, n=27	10.59–12.13, n=27
O. martiensseni (females)						
Adult specimens	25.5 ± 0.38	8.3 ± 0.23	12.8 ± 0.20	13.2 ± 0.24	5.9 ± 0.18	10.8 ± 0.22
	24.77–26.06, n=26	7.81–8.50, n=26	12.45–13.05, n=26	12.73–13.58, n=26	5.71–6.10, n=26	10.21–11.12, n=26
O. madagascariensis (males)[1]	25.7 ± 0.48	8.2 ± 0.20	12.7 ± 0.22	12.8 ± 0.26	5.4 ± 0.22	10.5 ± 0.25
	26.53 – 28.85, n=18	7.85–8.50, n=18	12.22–13.04, n=18	12.27–13.24, n=18	4.98–5.82, n=18	10.07–10.88, n=18

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TABLE 2. (Continued)

Taxon	GSL	BCH	MB	ZB	IOW	BCB
O. madagascariensis (females)						
Holotype MNHN 1985-1590	23.8	8.2	11.9	12.0	5.0	10.5
Other specimens	23.7 ± 0.50	7.9 ± 0.17	12.0 ± 0.24	12.1 ± 0.25	5.1 ± 0.15	10.1 ± 0.28
	22.83–24.51, n=19	7.59–8.22, n=19	11.50–12.36, n=19	11.57–12.58, n=19	4.87–5.38, n=19	9.65–10.60, n=19
O. wroughtoni (males)						
Other specimens including paratypes	24.0 ± 1.09	8.8 ± 0.21	12.6 ± 0.20	13.3 ± 0.22	6.3 ± 0.27	10.8 ± 0.18
	23.24–24.78, n=2	8.60–8.89, n=2	12.41–12.69, n=2	13.10–13.41, n=2	6.08–6.46, n=2	10.69–10.95, n=2
O. wroughtoni (females)						
Holotype BM 12.11.24.1	24.8	8.8	12.9	13.3	6.2	11.2
Other specimens	24.2 ± 0.30	8.6 ± 0.07	12.4 ± 0.22	12.7 ± 0.14	6.1 ± 0.03	11.0 ± 0.05
	23.99–24.51, n=3	8.47–8.60, n=3	12.23–12.66, n=3	12.59–12.86, n=3	6.07–6.13, n=3	10.90–10.96, n=3
O. formosus (male)						
Holotype RMNH 15322[2]	23.0	–	12.4	12.4	–	10.8
Other specimens	21.5 ± 1.12	7.7 ± 0.49	11.0 ± 0.84	11.1 ± 0.68	5.1 ± 0.33	9.6 ± 0.45
	20.68–22.27, n=2	7.39–8.08, n=2	10.39–11.58, n=2	10.66–11.62, n=2	4.89–5.36, n=2	9.27–9.91, n=2
O. formosus (female)						
Paratype[1]	23.3	_	12.5	12.5	_	10.4
O. papuensis (male)						
Adult specimen (BMNH 73.136)	19.5	7.5	10.6	10.4	5.2	9.5
O. papuensis (female)						
Holotype MCZ 45769[3]	20.2	–	10.4	10.6	–	9.5
O. johnstonei (male only, no data available for females)						
Holotype M 37986[2]	23.0	43.7	11.6	11.7	–	10.4
O. secundus (male)						
Holotype BMNH 50.982	21.2	7.4	11.5	11.1	5.1	9.8
O. secundus (females)	21.3 ± 0.13	7.6 ± 0.22	11.1 ± 0.08	11.2 ± 0.02	4.9 ± 0.01	10.2 ± 0.11
Paratypes represented in this study	21.21–21.40, n=2	7.45–7.76, n=2	11.08–11.20, n=2	11.15–11.18, n=2	4.91–4.93, n=2	10.16–10.31, n=2

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TABLE 2. (Continued)

Taxon	PL	MTR	UCW	LTR	MAT	TBL
O. harrisoni **sp. nov.** (males)						
Holotype HZM 60.36217	11.6	10.8	3.4	11.6	5.4	7.1
Paratypes	11.0 ± 0.26	10.4 ± 0.31	3.1 ± 0.02	11.2 ± 0.29	5.1 ± 0.04	7.2 ± 0.27
	10.75–11.26, n=3	10.23–10.78, n=3	3.05–3.08, n=3	10.96–11.52, n=3	5.10–5.18, n=3	6.89–7.37, n=3
Other referred specimens	11.6 ± 0.21	10.5 ± 0.21	3.2 ± 0.18	11.4 ± 0.19	5.4 ± 0.14	7.0 ± 0.16
	11.23–12.02, n=34	10.13–10.99, n=34	2.88–3.66, n=34	11.01–11.83, n=34	5.18–5.74, n=34	6.70–7.50, n=34
O. harrisoni **sp. nov.** (females)						
Paratypes	10.7 ± 0.18	10.0 ± 0.11	3.0 ± 0.19	10.6 ± 0.24	5.1 ± 0.07	6.8 ± 0.17
	10.47–11.04, n=9	9.83–10.21, n=9	2.70–3.23, n=9	10.14–10.97, n=9	5.0–5.24, n= 9	6.43–7.04, n=9
Other referred specimens	10.8 ± 0.30	10.0 ± 0.24	2.9 ± 0.18	10.7 ± 0.20	5.1 ± 0.14	6.8 ± 0.20
	10.21–11.27, n=32	9.53–10.50, n=32	2.43–3.25, n=32	10.28–11.05, n=32	4.88–5.39, n=32	6.42–7.13, n=32
O. martiensseni (males)						
Holotype MNHU 97523	11	10.2	3.4	11.1	5.3	6.7
Other specimens	11.2 ± 0.49	10.2 ± 0.36	3.2 ± 0.27	11.1 ± 0.33	5.4 ± 0.26	6.7 ± 0.20
	10.41–12.00, n=27	9.69–10.66, n=27	2.75–3.60, n=27	10.55–11.55, n=27	4.93–5.70, n=27	6.25–7.10, n=27
O. martiensseni (females)						
Adult specimens	10.3 ± 0.28	9.5 ± 0.19	2.9 ± 0.18	10.2 ± 0.24	5.0 ± 0.14	6.4 ± 0.20
	9.84–10.78, n=26	9.22–9.98, n=26	2.66–3.26, n=26	9.84–10.73, n=26	4.65–5.10, n=26	6.06–6.84, n=26
O. madagascariensis (males)[1]	10.3 ± 0.25	9.5 ± 0.25	2.8 ± 0.24	10.1 ± 0.21	4.8 ± 0.18	6.3 ± 0.26
	9.99–10.78, n=18	9.08–9.98, n=18	2.43–3.23, n=18	9.67–10.43, n=18	4.43–5.11, n=18	5.87–6.73, n=18
O. madagascariensis (females)						
Holotype MNHN 1985-1590	9.5	8.8	2.4	9.1	4.3	6.2
Other specimens	9.3 ± 0.28	8.8 ± 0.21	2.5 ± 0.14	9.2 ± 0.14	4.3 ± 0.14	6.0 ± 0.24
	8.67–9.71, n=19	8.40–9.11, n=19	2.30–2.78, n=19	8.71–9.57, n=19	4.02–4.50, n=19	5.56–6.52, n=19

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TABLE 2. (Continued)

Taxon	PL	MTR	UCW	LTR	MAT	TBL
O. wroughtoni (males)						
Other specimens including paratypes	9.1 ± 0.04	8.7 ± 0.04	2.6 ± 0.05	9.3 ± 0.10	4.57 ± 0.01	6.4 ± 0.22
	9.04–9.10, n=2	8.70–8.75, n=2	2.60–2.67, n=2	9.18–9.32, n=2	4.56–4.57, n=2	6.23–6.54, n=2
O. wroughtoni (females)						
Holotype BM 12.11.24.1	9.3	8.9	2.7	9.7	5	6.4
Other specimens	9.0 ± 0.20	8.7 ± 0.18	2.8 ± 0.18	9.5 ± 0.12	4.4 ± 0.06	6.5 ± 0.06
	8.79–9.18, n=3	8.48–8.83, n=3	2.59–2.94, n=3	9.38–9.61, n=3	4.37–4.49, n=3	6.42–6.53, n=3
O. formosus (male)						
Holotype RMNH 15322[2]	8.0	9.1	–	–	–	6.0
Other specimens	8.1 ± 0.63	7.7 ± 0.43	3.4 ± 0.23	8.1 ± 0.42	3.9 ± 0.44	5.5 ± 0.28
	7.66–8.55, n=2	7.37–7.98, n=2	3.20–3.53, n=2	7.81–8.41, n=2	3.62–4.24, n=2	5.27–5.67, n=2
O. formosus (female)						
Paratype[1]	8.5	–	–	–	–	5.7
O. papuensis (male)						
Adult specimen (BMNH 73.136)	7.7	6.9	1.9	7.4	3.5	4.9
O. papuensis (female)						
Holotype MCZ 45769[3]	–	–	–	7.7	–	–
O. johnstonei (male only, no data available for females)						
Holotype M 37986[2]	8.2	8.9	–	–	–	6.6
O. secundus (male)						
Holotype BMNH 50.982	7.6	7.3	2.5	7.8	4	5.6
O. secundus (females)	8.2 ± 0.04	7.0 ± 0.52	2.3 ± 0.11	7.8 ± 0.03	4.0 ± 0.02	5.6 ± 0.02
Paratypes represented in this study	8.17–8.22, n=2	6.64–7.37, n=2	2.23–2.38, n=2	7.79–7.83, n=2	4.01–4.04, n=2	5.58–5.60, n=2

[1] Richards *et al.* (2012), [2]Kitchener *et al.* (1992); [3] Lawrence (1948)

TABLE 3. Factor loadings of 12 craniodental variables on the first three principal components for *Otomops*. Principal component analyses were conducted using the variance-covariance matrices of $\log_{10}$-transformed variables of males and females. Loading values in bold indicate craniodental variables with factor loading values > 0.750.

Craniodental measurement	Males (n = 89)			Females (n = 93)		
	PC1	PC2	PC3	PC1	PC2	PC3
Greatest skull length	**0.819**	0.489	0.255	0.612	0.712	0.300
Braincase height	0.411	**0.797**	0.278	**0.771**	0.496	0.188
Mastoid breadth	0.713	0.605	0.207	0.680	0.625	0.339
Zygomatic breadth	0.704	0.635	0.260	0.657	0.598	0.417
Inter-orbital width	0.384	**0.836**	0.279	**0.810**	0.384	0.383
Braincase breadth	0.524	**0.758**	0.178	**0.853**	0.368	0.194
Palatal length	0.869	0.378	0.254	0.415	**0.836**	0.304
Maxillary toothrow length	0.840	0.439	0.257	0.442	**0.829**	0.264
Maxillary inter-canine width	0.310	0.286	**0.906**	0.247	0.300	**0.918**
Mandibular toothrow length	**0.838**	0.456	0.252	0.534	0.741	0.362
Moment arm of the temporalis	**0.819**	0.387	0.315	0.552	0.624	0.459
Tympanic bulla length	0.654	0.640	0.222	0.693	0.525	0.242
Variance explained (%)	83.948	4.977	4.856	84.583	5.215	3.716

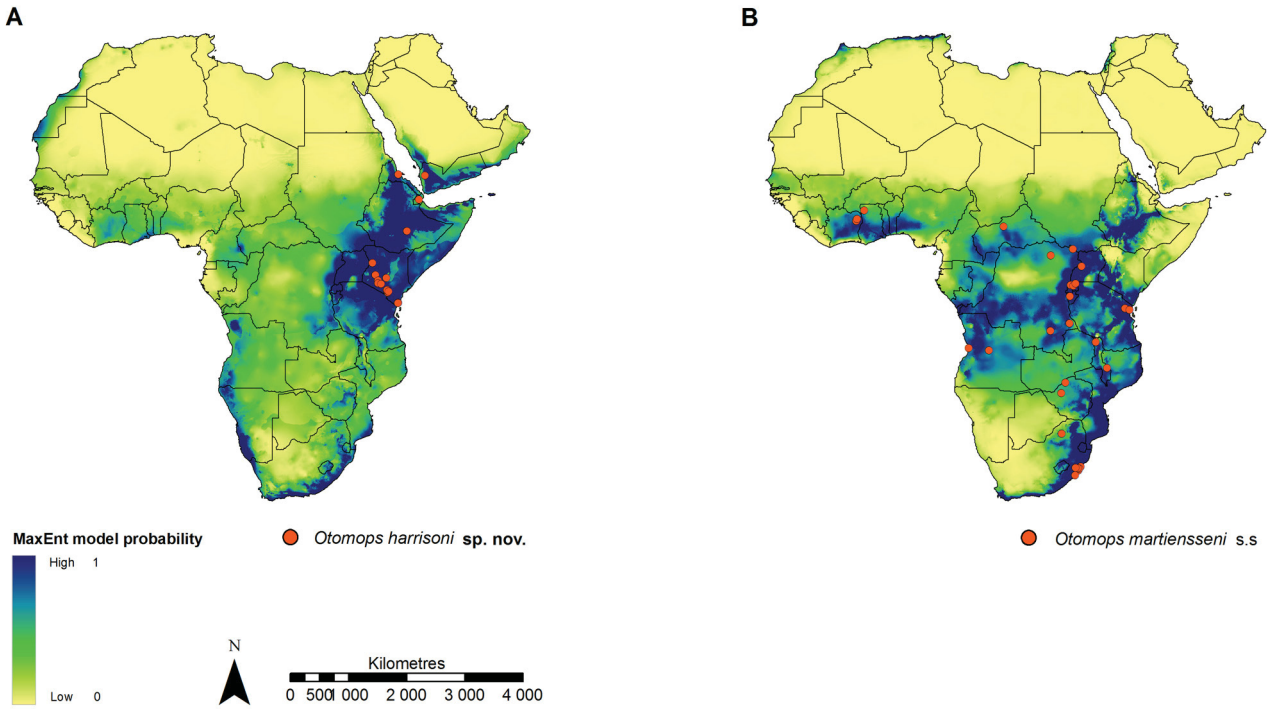

FIGURE 7. Occurrence probability for *Otomops harrisoni* **sp. nov.** (A) and *O. martiensseni* s.s. (B) in Africa and the Arabian Peninsula. Ecological niche models were generated based on current altitude and bioclimatic variables, and known occurrence records (indicated by the orange circles) for each species. Shading depicts the various grades of occurrence probability (based on habitat suitability), ranging from low (0) to high (1.00) suitability.

Ecological niche modelling. According to MaxEnt analysis, *O. harrisoni* is likely to occur mostly within the eastern regions of the sub-Saharan African mainland, including Kenya and Ethiopia, extending into Eritrea and the Arabian Peninsula (Fig. 7A). The distribution of *O. harrisoni* appears to be limited by the bioclimatic variables ALT1 (altitude), BIO4 (temperature seasonality), BIO12 (annual precipitation) and BIO14 (precipitation of driest month). Temperature seasonality limits potentially suitable habitat of *O. harrisoni* since values deviating from the

ideal result in steep declines in presence probability indicating that this species is better suited to a more stable bioclimate. This species also shows a preference for more than >20 mm of precipitation in the driest month, altitudes above 1500 m and annual precipitation below 500 mm.

Modelling results for *O. martiensseni* s.s. reveal a more extensive pattern of probable occurrence in the African region including: the coastal regions of South Africa, extending further north on the east coast through to Mozambique and eastern Tanzania, Uganda, Rwanda, Burundi and into Kenya and central Ethiopia (Fig. 7B). The potential distribution range also includes parts of the Democratic Republic of Congo in central Africa, and, further west, areas of Ivory Coast, Ghana, Togo, Benin and southwest Nigeria. Probabilities decrease as the range approaches the drier climes of the Saharan region and the Namib Desert. Distribution is mainly affected by variables BIO12 (annual precipitation), BIO14 (precipitation of the driest month) and BIO13 (precipitation of the wettest month). Areas with relatively lower annual precipitation levels (<1000 mm) present unsuitable habitats for *O. martiensseni* s.s. whereas optimal precipitation for the driest (0–40 mm) and wettest (~175 mm) months result in higher presence probabilities. Deviations from the optimum result in relatively steep declines in habitat suitability.

MaxEnt models show overlap in the potential distribution of both *Otomops martiensseni* s.s. and *O. harrisoni* in parts of Kenya, Ethiopia, Uganda and Tanzania. Annual precipitation influences the distribution of each species in contrasting ways. *Otomops harrisoni* appears more suited to drier climes, as the occurrence probability decreases as rainfall increases above 500 mm per year, whereas *O. martiensseni* s.s. appears better suited for wetter conditions, as presence probabilities decrease as rainfall decreases below 1000 mm per year. *Otomops harrisoni* appears to prefer higher altitudes, as habitat suitability decreases with altitudes below 1500 m. In contrast, *Otomops martiensseni* s.s. shows a slight drop in presence probability with increasing altitude (above sea level), however presence probability remains above 60% even at altitudes above 4000 m. Precipitation of the wettest month is a limiting factor for *O. martiensseni* s.s. and precipitation of the driest month are limiting factors for both *O. harrisoni* and *O. martiensseni* s.s.

Systematics

Family Molossidae Gervais, 1856

Genus *Otomops* Thomas, 1913

Otomops harrisoni sp. nov.

Harrison's large-eared giant mastiff bat
Figures 8–10

Synonymy

Otomops martiensseni martiensseni: Harrison, 1965:2 (part)
Otomops martiensseni martiensseni: Hill and Morris, 1971:46
Otomops martiensseni: Đulic and Mutere, 1973:62 (part)
Otomops martiensseni: Kinoti, 1973:129
Otomops martiensseni: Mutere, 1973:83
Otomops martiensseni: Epelu-Opio, 1974:229
Otomops martiensseni martiensseni: Largen *et al*., 1974:250
Otomops martiensseni: Kingdon, 1974:338 (part)
Otomops martiensseni: Warner *et al*., 1974:171 (part)
Otomops martiensseni: Kayanja and Mutere, 1975:166
Otomops martiensseni: Kayanja and Mutere, 1978:245
Otomops martiensseni: Valdivieso *et al*., 1979:6
Otomops martiensseni: Freeman, 1981:61 (part)
Otomops martiensseni: Norberg, 1981:365 (part)
Otomops martiensseni martiensseni: Aggundey and Schlitter, 1984:144
Otomops martiensseni: Fenton and Crerar, 1984:398
Otomops martiensseni: Freeman, 1984:400 (part)
Otomops martiensseni: Hickey and Fenton, 1987:381
Otomops martiensseni: Norberg, 1987:53 (part)
Otomops martiensseni: Norberg and Rayner, 1987:plate 1 (part)

Otomops martiensseni: Thollesson and Norberg, 1991:26 (part)
Otomops martiensseni: Long, 1995:1 (part)
Otomops martiensseni: Peterson *et al*., 1995:178 (part)
Otomops martiensseni: Yalden *et al*., 1996:91 (part)
Otomops martiensseni: Rydell and Yalden, 1997:72 (part)
Otomops martiensseni: Al-Jumaily, 1999:241
Otomops martiensseni: Monath, 1999:S130 (part)
Otomops martiensseni: Pearch *et al*., 2001:388
Otomops martiensseni: Debaeremaeker and Fenton, 2003:221 (part)
Otomops martiensseni: Jones and Rydell, 2003:303 (part)
Otomops martiensseni: Kock and Zinner, 2004:3
Otomops martiensseni: Kock *et al*., 2005:2
Otomops martiensseni: Taylor *et al*., 2005:26 (part)
Otomops martiensseni: Lamb *et al*., 2006:46 (part)
Otomops martiensseni: Lamb *et al*., 2008:25 (part)
Otomops martiensseni: Tong *et al*., 2009:483 (part)
Otomops martiensseni: Benda *et al*., 2011:25 (part)
Otomops martiensseni: Lamb *et al*., 2012:8 (part)
Otomops martiensseni: Patterson and Webala, 2012:5 (part)
Otomops martiensseni: Richards *et al*., 2012:913 (part)
Otomops martiensseni: Taylor *et al*., 2012:56 (part)
Otomops martiensseni: Kading *et al*., 2013:2394 (part)
Otomops martiensseni: Ralph and Lamb, 2013:4234 (part)
Otomops martiensseni: Tao *et al*., 2013:739 (part)
Otomops martiensseni: Yalden and Happold, 2013:480 (part)
Otomops martiensseni: Conrardy *et al*., 2014:259 (part)
Otomops martiensseni: Kassahun *et al*., 2015:168 (part)
Otomops martiensseni: Mortlock *et al*., 2015:1841 (part)

Holotype. HZM 60.36217 (field number A51) is part of a series of specimens collected by Paul J. J. Bates, M. J. Pearch and O. Nurhussein on 19 July 1998. This is an adult male presently preserved in 70% alcohol. The cranium and baculum have been extracted and prepared. External and craniodental measurements are presented in Tables 1 and 2, respectively. The cranium and mandible of the holotype are in good condition and are presented in figure 8. The baculum of the holotype was prepared following the methods of Hill & Harrison (1987) and Kearney *et al*. (2002), with slight modifications, and is illustrated in figure 9. This specimen was included in the morphological and mitochondrial DNA sequence-based analyses.

Type locality. Ethiopia, Bale District, Sof Omar Cave 06°54´N; 40°48´E; elevation 1340 m.

Paratypes. Thirteen adult specimens were collected from the same locality and on the same date as the holotype (n = 3 males, HZM 40.31315, HZM 44.31328, HZM 64.36221; n = 10 females, HZM 41.31316, HZM 42.31317, HZM 43.31318, HZM 56.36213, HZM 57.36214, HZM 58.36215, HZM 59.36216, HZM 61.36218, HZM 62.36219 (also DM 14750), HZM 63.36220). Measurements are provided in Tables 1–2.

Referred Specimens. Specimens originating from Djibouti, Eritrea, Ethiopia, Kenya and Yemen have been assigned to this taxon, as supported by molecular DNA and/or cranial morphological datasets, or based upon geographical location. Those specimens in bold have not been sequenced and their assignment to *O. harrisoni* is based on cranial morphological analyses alone. Djibouti: **BMNH 69.1256**, Day Forest National Park, Mount Day (11.767° N, 42.650° E, altitude 1400 m); Ethiopia: **HZM 45.31369**, **HZM 46.31370**, HZM 47.31371, **HZM 48.31372**, **HZM 49.33964**, **HZM 50.33965**, **SMF 41832**, **SMF 41833**, Bale District, Sof Omar Cave (6.900° N, 40.859° E, altitude 1300 m); Kenya: **ROM 48654–48657**, **ROM 48659–48664**, **ROM 48666–48667**, **ROM 63772**, **ROM 63779**, **ROM 63782**, **ROM 63808**, 19 km W of Makindu **(**2.300° S, 37.677° E, altitude 1000 m); **MRAC 38546–38549**, **SMNS 46077**, **SMNS 46079**, Chyulu Hills (2.583° S, 37.833° E, altitude 1930 m); **ROM 65875–65879**, Ithundu Caves, Kiboko (2.199° S, 37.717° E, altitude 920 m); **ROM 81198–81199**, Ithundu Caves, Makindu (2.333° S, 37.699° E, altitude 1100 m); **ROM 68360, ROM 68362, ROM 68364, ROM 68366**, Lake Baringo, Kampi Ya Moto (0.183° N, 35.867° E, altitude 1200 m); **MRAC 35264**, Machakos District (1.517° S, 37.267° E, altitude 1630 m); **ROM 78155–78158**, Makindu Cave, Makindu (2.300° S, 37.833° E, altitude 1000 m); **ROM 65873**, Makindu River (precise locality not defined); **ROM 36517**, **ROM 36519**, **ROM 41920**, **ROM 41924**, **ROM 41927–41928**, **ROM 41932**, **ROM 78147–78148**, **ROM 78151–78152**, **ROM 78154**, **ROM 91249–**

91250, Mount Suswa (1.150° S, 36.350° E, altitude 1895 m); **ROM 79677**, Nairobi (1.280° S, 36.817° E, altitude 1685 m); Yemen: **HZM 39.31195, HZM 51.33976,** HZM 52.33977, **HZM 53.33978, HZM 54.33979, HZM 55.33980,** NMP 91811–91816, **SMF 87648–87649,** SMF 87650, Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet (15.483° N, 43.533° E, altitude 2150 m).

Etymology. This species is named after the late renowned mammalogist, taxonomist and bat expert Dr. David L. Harrison (1926–2015). Harrison's numerous publications on Afro-Arabian Chiroptera, in particular the Molossidae, have significantly improved our knowledge of this poorly known family.

FIGURE 8. Cranium and mandible of the holotype of *Otomops harrisoni* **sp. nov.** (HZM 60.6217) in dorsal, ventral and lateral views. Scale bars = 10 mm. (Photographs taken by L.R. Richards).

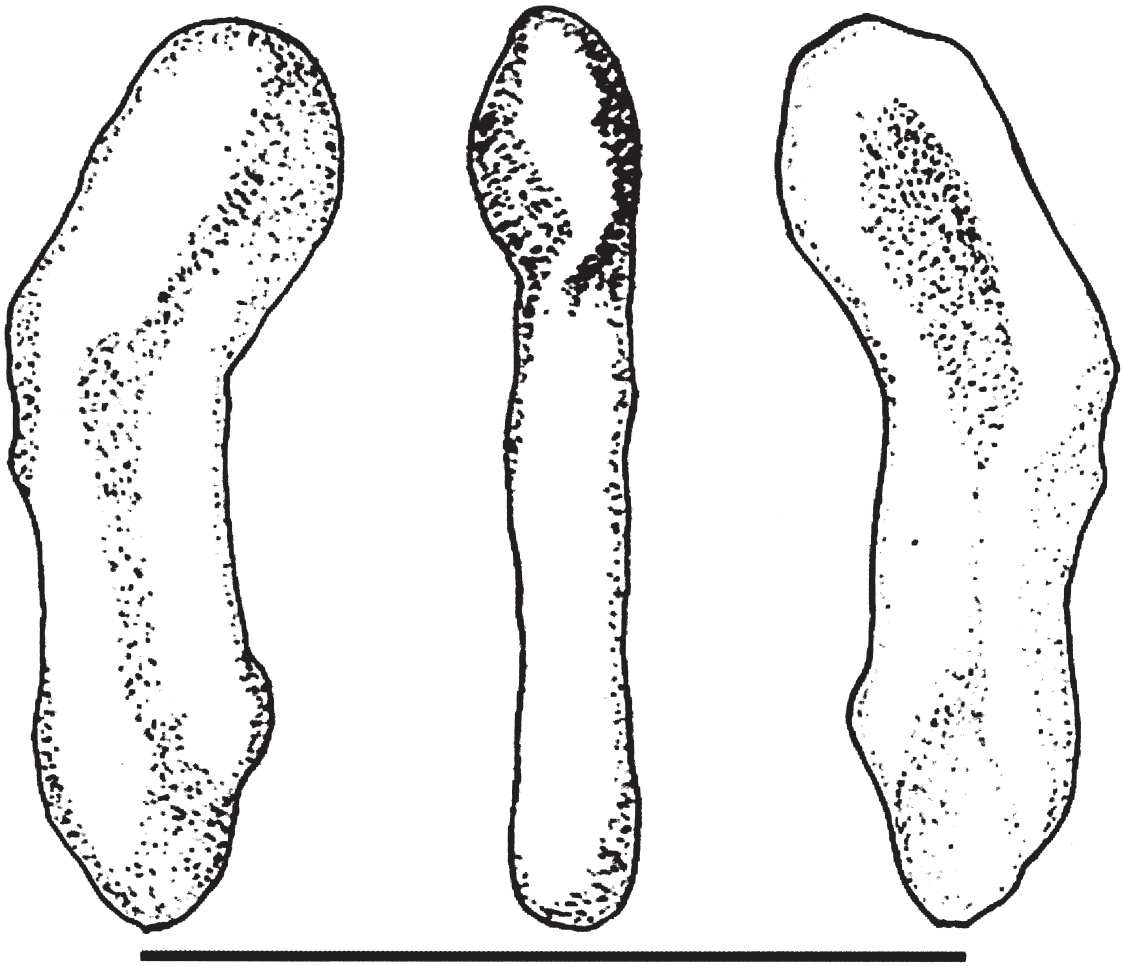

FIGURE 9. Dorsal, lateral and ventral views (from left to right) of the baculum of *Otomops harrisoni* **sp. nov.** holotype (HZM 60.36217). Scale bar = 1 mm.

Diagnosis. Diagnosis is based on statistically supported morphological differences and the occurrence of strongly supported reciprocally monophyletic lineages observed in analyses of concatenated mitochondrial cytochrome *b* and D-loop DNA sequences. Three lineages were strongly-supported within the Afro-Malagasy region; *O. madagascariensis* was sister to the reciprocally-monophyletic sister lineages, *O. martiensseni* s.s. and *O. harrisoni* (Fig. 2). *Otomops harrisoni* is separated from *O. martiensseni* s.s., its sister lineage, by a genetic p-distance of 2.10%, and from *O. madagascariensis* by 3.40%. *Otomops harrisoni* is further diagnosed by unique molecular characteristics, i.e. strict synapomorphies in both the cytochrome *b* gene and the D-loop region (Table 4).

In general, *O. harrisoni* is the largest and most robust member of the genus *Otomops* Thomas, 1913, overlapping in certain external and craniodental measurements with *O. martiensseni* s.s. The pelage is short and velvety, appearing dark chocolate brown on the upper parts, with a distinct cream-coloured collar that extends from the nape of the neck to the back. The ventral pelage consists of lighter brown-coloured hairs; it extends to the wings and covers a section of the plagiopatagium. The borders of the body and wing membranes of both the dorsal and ventral surfaces are marked by a distinct yet thin band of white fur, extending from the mid-humerus to the upper reaches of the thigh. Ears are long (35.2–46.0 mm for males, 33.6–41.0 mm for females), forward-directed and are united by a flap of skin across the nose. The species is sexually dimorphic, with males characterised by an average forearm length of 70.7 ±1.91 mm (64.0–74.0 mm, n = 41), whereas in females the average forearm length is 69.5 ±1.62 mm (65.7–72.7 mm, n = 38).

In general, *O. harrisoni* can be distinguished from other Afro-Malagasy taxa by its long cranium and notably high braincase (Fig. 8). *Otomops harrisoni* is characterised by an average greatest skull length of 28.5 ±0.36 mm

(27.8–29.3 mm, n = 38) and 27.0 ±0.36 mm (26.2–27.9 mm, n = 41), for males and females, respectively. The height of the braincase (excl. the tympanic bullae) of males averages 9.4 ±0.18 mm (9.0–9.8 mm, n = 38) and females average 9.1 ±0.17 mm (8.7–9.5 mm, n = 41). There is distinct and comparatively deep depression across the fronto-parietal area of the braincase. The braincase is markedly domed in the frontal region. The lambdoidal crests are moderately developed, join to form a "V-pattern", and extend to the sagittal crest at the highest point of the cranium. The sagittal crest remains slightly pronounced along the fronto-parietals, terminating at the posterior edge of a depression in the inter-orbital region. The rostrum is broad and robust, with fairly large, laterally flared nasals. The jugal process of the zygomatic arch is thickened and the zygomaxillary junction projects outwards. The external tympanic bullae are elongate and posteriorly broadened; they extend to the pterygoids and occupy a third of the braincase. The baculum of the holotype of *O. harrisoni* measures 1.16 mm (Fig. 9). The maximum width of the baculum shaft (SW) is 0.29 mm. The inflection of the baculum shaft (IB) in both the dorsal and ventral views is 54.53°.

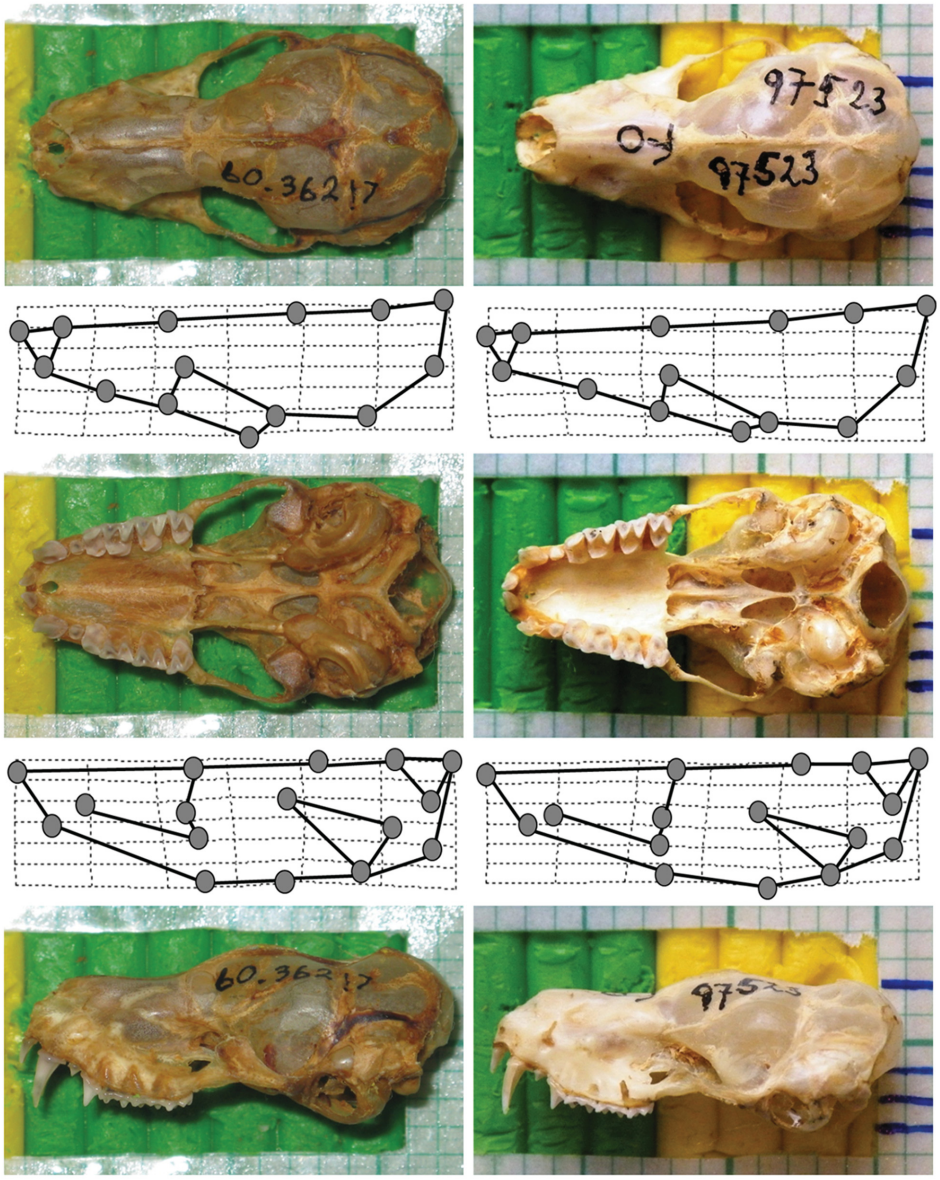

FIGURE 10. Comparative cranial views of the holotypes of *Otomops harrisoni* **sp. nov.** (HZM 60.36217), from Sof Omar Cave, Ethiopia on the left and *O. martiensseni* s.s. (MNHU 97523), from the foothills of the Usambara Mountains, near Tanga, Tanzania on the right. Thin plate splines illustrating the cranial morphology of *O. harrisoni* **sp. nov.** and *O. martiensseni* s.s., exaggerated 3x, are provided for the dorsal and ventral views.

TABLE 4. Unique synapomorphies of *O. harrisoni* **sp. nov.** in the mitochondrial cytochrome *b* gene and D-loop region. The first nucleotide gives the ancestral state, followed by the nucleotide position in each sequence, and the last nucleotide gives the derived state.

Haplotype number	Cytochrome *b*	D-loop
31	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	A(4)T; A(6)G; C(41)T; C(58)T; A(59)C; A(101)G; -(131)A; T(140)C; A(142)G; G(144)A; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; C(220)T; A(235)G; G(250)A; C(252)T; T(264)C
32	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; A(80)G; T(119)C; -(131)G; T(140)C; G(144)A; A(160)G; T(167)C; T(168)C; A(177)G; T(182)C; T(192)C; C(200)T; T(202)C; T(205)G; C(220)T; G(250)A; T(264)C
33	T (85) C; C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)G; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; A(80)G; T(119)C; -(131)G; T(140)C; G(144)A; A(160)G; T(167)C; T(168)C; A(177)G; T(182)C; T(192)C; C(200)T; T(202)C; T(205)G; C(220)T; G(250)A; T(264)C
34	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)G; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; -(131)G; T(140)C; A(142)G; G(144)A; A(160)G; T(167)C; A(177)G; T(182)C; T(190)C; A(191)G; C(200)T; T(202)C; T(205)G; C(220)T; C(252)T; G(250)A; T(264)C
35	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)G; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; -(131)G; T(140)C; A(142)G; G(144)A; A(160)G; T(167)C; A(177)G; T(182)C; T(190)C; C(200)T; T(202)C; T(205)G; C(220)T; G(250)A; C(252)T; T(264)C
36	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(798)C; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; A(6)G; T(25)C; C(41)T; C(58)T; A(59)C; G(81)A; A(101)G; -(131)A; T(140)C; A(142)G; G(144)A; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; C(220)T; A(221)G; A(235)G; G(250)A; C(252)T; T(264)C
37	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(798)C; T(810)C; T(831)C; C(837)T; T(933)C	A(4)T; T(5)C; A(15)G; C(41)T; A(59)T; -(131)G; T(140)C; A(142)G; G(144)A; T(166)C; G(176)A; A(177)G; T(182)C; A(195)G; C(200)T; T(202)C; T(205)A; A(206)G; C(220)T; G(250)A; T(264)C
38	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; -(131)G; T(140)C; A(142)G; G(144)A; A(160)G; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; C(220)T; A(221)G; G(250)A; C(252)T; T(264)C
39	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; G(304)A; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(798)C; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; A(101)G; -(131)G; T(140)C; G(144)A; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; G(250)A; C(252)T
40	C(231)T; G(232)A; C(243)A; A(258)C; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; A(101)G; -(131)G; T(140)C; A(142)G; G(144)A; A(160)G; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; C(220)T; G(250)A; C(252)T; T(264)C

.....continued on the next page

TABLE 4. (Continued)

Haplotype number	Cytochrome *b*	D-loop
41	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; C(564)T; A(651)G; T(664)C; A(786)G; T(798)C; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; A(101)G; -(131)G; A(142)G; G(144)A; A(160)G; T(167)C; A(169)G; A(177)G; T(182)C; C(200)T; T(202)C; T(205)A; C(220)T; A(230)G; T(231)C; G(250)A; C(252)T; T(264)C
42	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(8)T; C(41)T; C(58)T; A(59)C; A(105)G; A(126)G; -(131)G; T(140)C; G(144)A; A(160)G; T(167)C; C(172)T; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; C(220)T; A(230)G; G(250)A; C(252)T; T(264)C
43	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; A(6)G; C(41)T; C(58)T; A(59)C; G(81)A; A(101)G; -(131)A; T(140)C; A(142)G; G(144)A; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; A(221)G; G(250)A; C(252)T; T(264)C
44	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(798)C; T(810)C; T(831)C; C(837)T; T(933)C	A(4)T; C(41)T; C(58)T; A(59)T; A(101)G; -(131)G; A(142)G; G(144)A; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)A; C(220)T; A(230)G; G(250)A; C(252)T; T(264)C
45	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; A(6)G; C(41)T; C(58)T; A(59)C; G(81)A; -(131)A; T(140)C; A(142)G; G(144)A; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; A(214)G; C(220)T; A(221)G; A(235)G; G(250)A; C(252)T; T(264)C
46	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; -(131)G; T(140)C; A(142)G; G(144)A; A(160)G; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; C(220)T; A(221)G; G(250)A; C(252)T; T(264)C
47	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; T(627)C; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)C; A(59)T; A(101)G; -(131)G; T(140)C; G(144)A; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; C(220)T; G(250)A; C(252)T
48	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; G(304)A; C(336)G; A(426)G; C(564)T; T(627)C; A(651)G; T(664)C; A(786)G; T(798)C; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; -(131)G; T(140)C; A(142)G; G(144)A; A(160)G; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)G; C(220)T; A(221)G; G(250)A; C(252)T; T(264)C
49	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; C(356)T; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; T(140)C; A(142)G; G(144)A; A(160)G; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; T(205)A; C(220)T; A(221)G; G(250)A; C(252)T; T(264)C
50	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; T(140)C; A(142)G; G(144)A; A(160)G; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; C(220)T; G(250)A; C(252)T; T(264)C
51	C(231)T; G(232)A; C(243)A; C(291)T; C(297)T; C(336)G; A(426)G; C(564)T; A(651)G; T(664)C; A(786)G; T(810)C; T(831)C; C(837)T; T(933)C	T(2)C; A(4)T; C(41)T; C(58)T; A(59)T; T(140)C; G(144)A; T(167)C; A(177)G; T(182)C; C(200)T; T(202)C; C(220)T; G(250)A; C(252)T

Description and comparisons. *Externals*. *Otomops harrisoni* bears all the external morphological diagnostic features of the genus as described by Thomas (1913) and subsequently refined by Freeman (1981). As with other *Otomops* spp. the pelage is conspicuous and is characterised by dark chocolate brown fur on the back and head, with slightly paler under parts. A cream-coloured collar extends from the dorsal surface of the neck to the throat, separating the head and back regions. This collar varies in size amongst the members of the genus. It is fairly pronounced in the Afro-Malagasy members (Monadjem *et al*. 2010; Goodman & Raherilalao 2014), and in some Indo-Australasian taxa (Thomas 1913; Kitchener *et al*. 1992), yet is reduced to a narrow pale band of hairs in *O. papuensis* (Lawrence 1948; Hill 1983). Characteristic of the genus, the large ears of *O. harrisoni* project forwards and join anteriorly above the nose. A series of brown spines is located along the anterior border of the ears (c. 15) and a flexible flange extends from the dorsal to the ventral surface of the pinnae; features shared by all *Otomops* spp. Similar to congenerics, the antitragus is absent and the tragus is minute. The two nostrils are stiffened by cutaneous ridges that run above and between them. These ridges are lined with small brown spines. The lips are characterised by loose folds and the anterior surface of the upper and lower lips are covered in short, light-brown bristles of hair. Common to other Afro-Malagasy and Indo-Australasian members, the upper lip projects beyond the lower lip. The feet of *O. harrisoni* are broad, with a comb of long white hairs. The ventral surfaces of the first and fifth toes are speckled with short light-coloured hairs. Adult males possess a distinct gular gland that is located on the lower portion of the throat. A similar gland has been reported from *O. martiensseni* s.s. (Chubb 1917), *O. madagascariensis* (Eger & Mitchell 2003), and *O. wroughtoni* (Thomas 1913). The first digit of *O. harrisoni* is noticeably thickened at its base and tapers to a point at the claw. Some individuals possess thumb pads that are slightly distended. A series of *O. martiensseni* s.s. examined from Durban displayed similar thumb pads; this feature appeared to be most pronounced in males. Based on external measurements, *O. harrisoni* is, in general, larger than other *Otomops* spp., including Afro-Malagasy congenerics. For instance, the average forearm length in *O. harrisoni* is 70.7 ±1.91 mm (63.8–74.0 mm, n = 41 males) and 69.5 ±1.62 mm (65.7–72.7 mm, n = 38 females), whereas in *O. martiensseni* s.s. this measurement is 65.8 ±1.60 mm (60.5–68.0 mm, n = 24 males) and 63.5 ±1.53 mm (60.0–66.3 mm, n = 22 females), and in *O. madagascariensis* average forearm length is 63.2 ±1.35 mm (60.0–66.0 mm, n = 20 males) and 61.2 ±1.32 mm (60.0–64.0 mm, n = 18 females).

Craniodental characters. The cranium of *O. harrisoni* is, in general, longer and broader relative to other Afro-Malagasy *Otomops* spp., yet there is some overlap in measurements with other Afro-Malagasy taxa, particularly *O. martiensseni* s.s. (Table 2). Given the morphological similarity between the two sister species, we have provided a side-by-side comparison of the crania of the holotypes of *O. harrisoni* and *O. martiensseni* s.s. to highlight the distinguishing features of the new species (Fig. 10). The average greatest skull length of *O. harrisoni* (males: 28.5 mm, range 27.8–29.3 mm; females: 27.1 mm, range 26.2–27.9 mm) is at least 1.04 times greater than the average greatest skull length of *O. martiensseni* s.s. (males: 27.5 mm, range 26.5–28.8 mm; females: 25.5 mm, range 24.7–26.1 mm), and 1.12 times that of *O. madagascariensi*s (males: 25.7 mm, range 24.9–26.5 mm; females: 22.8 mm, range 22.8–24.5 mm). Multivariate analysis of craniodental data, demonstrated that *O. harrisoni* can be separated from *O. martiensseni* s.s. and *O. madagascariensis* based on greater inter-orbital width, braincase breadth and braincase height. The braincase of *O. harrisoni* is overall larger and higher than other *Otomops* spp. including *O. martiensseni* s.s.; this is most visible in the lateral view (Fig. 10). There is minimal overlap in braincase height (excl. tympanic bullae) between the corresponding sexes of *O. harrisoni* (males: 9.0–9.8 mm; females: 8.7–9.5 mm) and *O. martiensseni* s.s. (males: 8.2–9.0 mm; females: 7.8–8.8 mm), and there is no overlap of *O. harrisoni* with *O. madagascariensis* (males: 7.9–8.5 mm; females: 7.9–8.2 mm). Compared to *O. martiensseni* s.s., the frontal region of the cranium of *O. harrisoni* is markedly more inflated giving it a dome-like appearance (Fig. 10). Conversely, *O. martiensseni* s.s. is characterised by a more anteriorly slanted frontal region, giving the braincase a lower lateral profile than *O. harrisoni.* The depression that lies across the fronto-parietal suture of the braincase is less pronounced in *O. martiensseni* s.s. than in *O. harrisoni.* The sagittal crest and lambdoidal crests are slightly more developed in *O. harrisoni* than in *O. martiensseni* s.s. and *O. madagascariensis*. They join above the occiputs to produce a "V-pattern", giving the occipital region a rounded appearance; a characteristic feature of the genus. In *O. harrisoni* the sagittal crest remains slightly pronounced along the fronto-parietals, terminating at the inter-orbital depression by the junction of the nasals and frontals. In *O. martiensseni* s.s. and *O. madagascariensis* this feature is poorly developed. The anterior portion of the rostrum is more expansive in *O. harrisoni* than in *O. martiensseni* s.s. and *O. madagascariensis*. The mastoid projections are well-developed, elongate and contribute to the rounded appearance of the braincase when the cranium is viewed dorsally. In the lateral view, the foramen

magnum of *O. harrisoni* is situated higher than in *O. martiensseni* s.s. The lacrimal process is distinct in most *Otomops* spp., but is particularly prominent in the Afro-Malagasy members including *O. harrisoni*. The jugal process of the zygomatic arch is thickened and the zygomaxillary junction is more laterally displaced than in *O. martiensseni* s.s. A prominent vertical process is located on the dorsal surface of the zygoma; it is slightly broader and rounder in appearance than in *O. martiensseni* s.s. and *O. madagascariensis*. The basisphenoid pits are elongate, oval-shaped, and deep. They appear to be wider in the holotype of *O. martiensseni* s.s. than in that of *O. harrisoni*. The broadened occipital condyles of the northeastern African species project outwards. The posterior border of the hard palate extends to the posterior margin of M^3, similar to *O. martiensseni* s.s. *Otomops harrisoni* has external tympanic bullae that are longer and more posteriorly inflated than *O. martiensseni* s.s.

Typical of the genus, the mandible is thin and gracile, ending in an outwardly deflected angular process. The coronoid process is low-lying and the mandibular condyle is positioned in line with the lower toothrow. There is a distinct tubercle on the mandibular ramus between the third molar and the coronoid process. This tubercle has been observed in all three Afro-Malagasy species and has been reported from some Indo-Australasian species (Kitchener *et al*. 1992). The dental formula of *O. harrisoni* is I 1/2, C 1/1, P 2/2, M 3/3, characteristic of molossid bats. The upper incisors are moderately-developed and are separated from the canines by a slight diastema. This diastema is present in *O. martiensseni* s.s. and *O. madagascariensis*. The upper canines are long and fairly robust. The upper anterior premolar is small, reaching slightly past the cingulum of the posterior premolar, whereas the lower anterior premolar is half the size of the posterior premolar. The first two upper molars are similar in size, whilst the third molar is smaller in size and bears an unreduced commissure. The lower molars decrease in size from M_1 to M_3.

Molecular analyses. Analyses conducted using both mitochondrial and nuclear data are in agreement with regard to the number of extant clades/clusters within the Afro-Malagasy region. Genetic structure inferred by microsatellite analysis suggests strong genetic structure at regional (SECW, NEA), rather than population or colony level, and little gene-flow between the SECW and NEA regions, the habitats of *O. martiensseni* s.s. and *O. harrisoni*, respectively. The three groups formed, namely SECW, NEA and MAD (Fig. 4), correspond to the clades observed in the phylogram generated using concatenated cytochrome *b* and D-loop data (Fig. 2), the networks constructed using concatenated nuclear intron data (Fig. 3), as well as results reported by Lamb *et al*. (2008) and Richards *et al*. (2012). Clade G, comprising Malagasy *Otomops* specimens classified as *O. madagascariensis*, shows distinct and strongly supported (bootstrap support: 100%; posterior probability: 1.00) separation from the clades from mainland Africa (Fig. 2). Genetically, the sister lineages from mainland Africa and the Arabian Peninsula separate to form two independent reciprocally-monophyletic clades (subclades E and F), each having strong bootstrap and posterior probability support. These sister lineages are separated by a genetic p-distance of 2.10%. Nuclear sequence data supports this separation where, in figure 3, all *Otomops* spp. form independent networks at 95% confidence limit. The designation of *O. martiensseni* s.s. and *O. harrisoni* as separate species is supported based on the separation of individuals from the African mainland into 2 distinct groups derived from mitochondrial and nuclear sequence data and nuclear microsatellites.

Biology, distribution and conservation status. As mentioned above, specimens originating from Djibouti, Eritrea, Ethiopia, Kenya and Yemen have been assigned to this taxon. Therefore observations based on previously published literature ascribed to northeast African individuals now applies to *O. harrisoni*. While bioacoustic information is available from the literature for *O. martiensseni* s.s. (Fenton & Bell 1981; Fenton *et al*. 2002, 2004; Adams *et al*. 2015) and *O. madagascariensis* (Russ *et al*. 2003), information on individuals attributable to *O. harrisoni* is uncertain. Limited time expansion recordings of a single hand-released individual captured at Bungule, Taita Hills in Kenya showed a frequency of maximum energy of 12.00 kHz, minimum frequency of 10.50 kHz, maximum frequency of 16.50 kHz, and a call duration of 9.00 ms (Taylor *et al*. 2005); recorded echolocation parameters that lie within the previously described ranges of *O. martiensseni* s.s. (Fenton & Bell 1981; Fenton *et al*. 2002, 2004; Adams *et al*. 2015) and *O. madagascariensis* (Russ *et al*. 2003). However, as Bungule is equidistant from the nearest sampled localities included within this study for both *O. harrisoni* (Chyulu Hills) and *O. martiensseni* s.s. (Usambara foothills), the taxonomic assignment of the Taita Hills individual is uncertain. To the best of our knowledge, no information on animals that can be definitively assigned to *O. harrisoni* is presently available.

Scat analysis of Ethiopian *Otomops* inferred that this is an insectivorous bat feeding predominantly (97% by volume) on medium (size range: 1–5 cm) to large (wing span size range: 2.5–30 cm) Lepidoptera of the moth

families Noctuidae, Geometridae and Saturniidae (Rydell & Yalden 1997; Heppner 2008). *Otomops* has a diet that chiefly comprises a single prey category and is thus highly specialized for moth predation through its jaw and tooth morphology, flight style and echolocation system (Freeman 1981; Rydell & Yalden 1997; Jones & Rydell 2003). *Otomops martiensseni* s.s. bears similar morphological features as they relate to jaw architecture (Harrison 1965; Monadjem *et al*. 2010). As with *O. harrisoni*, the diet of *O. martiensseni* s.s. is comprised mostly of Lepidoptera (MC Schoeman, pers. comm.). This is in sharp contrast to the diet of the insular *O. madagascariensis* that consists of varying proportions of Lepidoptera, Diptera and Coleoptera (Andriafidison *et al*. 2007).

The reproductive cycle of two *Otomops* populations in Kenya, corresponding to the known distribution of *O. harrisoni*, was investigated by Mutere (1973) at the sites of Suswa and Ithundu Caves. Results indicated that males reach sexual maturity around one year of age, weighing approximately 25 g, at which time a gular gland had developed. Sexual maturity in females is indicated by lactation and/or the presence of a foetus, at approximately one year of age and at a similar mass to males. The breeding season occurs once a year and pregnant bats were found from October through January, birthing mainly in December. Females have a gestation period of around 3 months and give birth to a single, hairless young. For more on the reproductive biology of *Otomops* individuals from Kenya, see Long (1995) and references therein.

Members of *O. harrisoni* are known from a variety of habitats in northeast Africa and the Arabian Peninsula, including woodlands and shrublands of the Arabian Peninsula and Eritrea; montane grasslands, woodlands and forests of Ethiopia; xeric grassland and shrublands of Djibouti; and the bushlands and thickets of Kenya (Peel *et al*. 2007). According to the MaxEnt analysis conducted in this study (Fig. 7A), this range may include additional localities within Uganda, northern areas of Tanzania and southern areas of Somalia. These bats are found at high altitudes (>1000 m a.s.l) characterised by relatively drier climes (<500 mm annual precipitation), including warm semi-arid, tropical savanna, warm desert and, in the case of the Ethiopian highlands, temperate oceanic climates (Peel *et al*. 2007). Given these preferences, individuals roost predominantly in mountain-associated cave systems and lava caves. *Otomops* is known to congregate in the lava caves of the Rift Valley at Mount Suswa as well as the Ithundu caves of the Chyulu Hills in Kenya (Kingdon 1974; Kock *et al*. 2005) and is also found in the Sof Omar karst cave system of Ethiopia (Largen *et al*. 1974), the Hud Sawa caves at the Al-Rayadi Al-Gharbi Mountains in Yemen (Al-Jumaily 1999), the Day Forest National Park at the Goda Massif Mountains in Djibouti (Hill & Morris 1971) and within a disused railway line tunnel near Asmara in Eritrea (Kock & Zinner 2004). *Otomops harrisoni* roost sites are dark and poorly-ventilated, and consist primarily of natural structures with varying numbers of access points, e.g. whereas the tunnel housing the Asmara railway line has only one entry point (Kock & Zinner 2004), the Sof Omar and Mount Suswa caves have over 30 entrances each (Gunn 2004).

Otomops are usually found roosting in large colonies, comprising smaller groups of several hundred, tightly-packed individuals. Colonies observed at the Sof Omar, Ithundu and well-studied Mount Suswa roosts have been estimated to contain up to 15 thousand individuals per site; however, it has been suggested that Mount Suswa colonies may exhibit migratory behaviour, periodically leaving the breeding site caves in which they are normally found (Largen *et al*. 1974; Kock *et al*. 2005). At the time of publication, Al-Jumaily (1999) recorded the number of individuals in the Hud Sawa caves to be approximately 1500. Numbers in the Eritrean colony are comparatively lower than other roosts, i.e. approximately 500 individuals, since the railway tunnel would have only become suitable for habitation after 1974, making this a relatively young colony (Kock & Zinner 2004).

The IUCN classification of currently-circumscribed *O. martiensseni* is given as "Near Threatened" (Mickleburgh *et al*. 2008) and possibly close to qualifying as "Threatened" as population numbers have decreased over time. In light of the recircumscription of *O. martiensseni*, and the description of a new species, *O. harrisoni*, the conservation of both of these species will have to be assessed in future studies. Ethiopia is signatory to a number of conventions including the Conservation of Migratory Species, which lists *Otomops* as a species of interest. Although the Bale Mountains (Bale Mountains National Park and the Sof Omar National Monument included) are protected, protection measures are not clearly defined (Vreugdenhil *et al*. 2012). The large colony at Mt Suswa in Kenya is subject to human disturbance within the caves and does not appear to be protected (Kock *et al*. 2005). A protected area in the Day Forest National Park was assigned, although there may be a failure to implement prescribed conservation measures as a result of internal unrest in Djibouti (Hutson *et al*. 2001; Magin 2001). Conservation initiatives for the protection of *Otomops* within Yemen and Eritrea are unknown.

Discussion

This paper describes a new Afro-Arabian species of *Otomops*, *O. harrisoni*, based on material obtained from the Sof Omar caves in Ethiopia. This new species, which occurs in apparent parapatry with *O. martiensseni* s.s., has been characterized using differences in both genetic (mitochondrial and nuclear sequence and nuclear microsatellite) and morphological (craniodental measurements and dorsal and ventral landmarks) data. Samples obtained from localities in Djibouti, Eritrea, Kenya and Yemen have also been assigned to this taxon. Although phylogenetic (Lamb *et al*. 2006, 2008) and morphometric (Richards *et al*. 2012) studies of Afro-Malagasy *Otomops* have been published, it is hoped that this more inclusive paper will be able to resolve the number of species of *Otomops* from mainland Africa and the Arabian Peninsula. It has been suggested that the two Afro-Arabian *Otomops* groupings could represent evolutionary significant units (Lamb *et al*. 2008), however here we elevate their status to that of separate species.

Phylogenetic structure among Afro-Malagasy *Otomops* reveals the clear separation of samples into three strongly-supported clades which correspond to the species *O. martiensseni* s.s., *O. harrisoni* and *O. madagascariensis*. The mitochondrial DNA divergence between *O. martiensseni* s.s. and *O. harrisoni*, although relatively low (2.10% for concatenated cytochrome *b* and D-loop data), is not unusual since other bat species, although distinct at the morphological level, also possess low mitochondrial inter-specific divergences among sister taxa based on analysis of the same DNA regions. For example Goodman *et al*. (2010) recognises the separation of a *C*. '*pumilus'* clade from *C. leucogaster* by a cytochrome *b* genetic distance of 2.29%. Although 2.3% is considered relatively low for an inter-specific distance (Baker & Bradley 2006), mitochondrial mutation rates exhibit substantial variation between mammalian families (Nabholz *et al*. 2008) which raises the possibility that the molossid mitochondrial mutation rate may be lower than that in other bat families (Goodman *et al*. 2010).

Both nuclear intron sequence (95% confidence) and microsatellite analysis show congruence with phylogenetic analyses of mtDNA sequences, whereby Afro-Malagasy *Otomops* samples separate into three distinct networks/groups matching those found in the phylogenetic tree. The genetic separation of Afro-Arabian *Otomops* into two separate species indicates a lack of gene flow between the sister clades, even though members of *Otomops* may be capable of long-distance migrations. For example, *Otomops* individuals have been recorded from Molema Bush Camp (Tuli Block, Botswana), and the northern regions of South Africa including Kruger National Park and Mapungubwe National Park (Adams *et al*. 2015), as well as Modimolle (this study) and Mabelingwe near Bela-Bela (E. Balona, pers. comm.), where no records had previously existed within >600 km. Our results support the fact that both *O. martiensseni* and *O. harrisoni* are most likely characterised by homogenous gene pools across their range, although additional sampling would be required to collect individuals from the entire potential ranges of both species**.** Although isolating mechanisms have not been clearly identified, findings suggest that separation may be as a result of limiting bioclimatic factors: *O. harrisoni* occurs in regions of higher altitudes and lower annual precipitation whereas *O. martiensseni* s.s., although comparatively unaffected by altitude, is associated with areas of higher annual precipitation (see also Richards *et al*. 2012). Additionally, there may be as yet unknown ecological/biological factors at play, since geographical isolation may not be a factor for a species capable of long distance flight. Contrasting habitat preferences may have created barriers between *O. martiensseni* s.s. and *O. harrisoni*, allowing for both their physical and genetic separation over time.

Otomops harrisoni represents the largest species of the genus. In the Afro-Malagasy context, *O. harrisoni* can easily be distinguished from *O. madagascariensis* based on its comparatively larger and essentially non-overlapping size, particularly as it relates to the cranium. The species closely resembles *O. martiensseni* s.s. in its external appearance, yet the two can be distinguished from one another based on cranial size and shape. Multivariate comparisons of craniodental measurements and cranial landmark data for males and females showed separation of individuals assigned as *O. harrisoni* and *O. martiensseni* s.s. Our principal component analyses of craniodental characters revealed that this separation was largely based on the magnitude of the braincase breadth, braincase height, and inter-orbital width, with values for *O. harrisoni* greater than those reported for *O. martiensseni* s.s. The multivariate analyses of Richards *et al*. (2012) also showed braincase height as an important variable in distinguishing *O. martiensseni* s.s. from individuals currently identified as *O. harrisoni*. In contrast to this study, Richards *et al*. (2012), based on canonical variates analyses of craniodental measurements, described the northeastern species with a proportionately narrower inter-orbital region relative to *O. martiensseni* s.s. However, this morphological feature is most applicable to *O. madagascariensis* and not *O. harrisoni* as univariate analyses

and descriptive statistics of craniodental characters showed that *O. harrisoni*, in general, has a greater inter-orbital width than other Afro-Malagasy taxa (Tables 2–3 in Richards *et al*. 2012; this study).

To the best of our knowledge, we provided the first description of the baculum of *O. harrisoni*. The bacula of most *Otomops* species have not yet been described and intraspecific variation in bacula morphology within the Afro-Malagasy taxa is unknown. Further investigation is warranted to determine whether or not this morphological feature can be used in the taxonomic diagnoses of the various species.

Findings from this study illustrate the advantages of using a combined approach, based on morphological and molecular (nuclear and mitochondrial) analyses, with regards to the identification and description of new cryptic species. Although the taxonomic status of Afro-Malagasy *Otomops* has been assessed in this paper, it would be prudent to increase taxonomic sampling from additional localities on the African continent, specifically from central and western Africa.

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APPENDIX 1. Sampled individuals of *Otomops* (n = 291) and outgroups (n = 8) used in molecular and morphometric analyses. Museum acronyms: BMNH—Natural History Museum; DM—Durban Natural Science Museum; FMNH—Field Museum of Natural History; HZM—Harrison Zoological Institute; MNHN—Muséum National d'Histoire Naturelle; MNHU—Museum für Naturkunde der Humboldt Universität; MRAC—Musée Royal Central Africa; NM—KwaZulu-Natal Museum; NMK—National Museum of Kenya; NMP—National Museum of the Czech Republic, Prague; NMZ—Livingstone Museum; ROM—Royal Ontario Museum; SMF—Senckenberg Museum; SMNS—Staatliche Museum für Naturkunde; TM—Ditsong Museum of Natural History; Field number acronyms: DBN—Durban genetic samples (wing punches); DP—Durban Pinetown genetic samples (wing punches); KZN—KwaZulu-Natal genetic samples (wing punches); PB—Pter Benda; SMG—Steven M. Goodman. Museum numbers in bold indicate samples used in nuclear microsatellite analysis, asterisks (*) indicate samples used for nuclear intron analysis and question mark (?) indicates that sex of the specimen is unknown.

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
Otomops harrisoni **sp. nov.**	Djibouti	Day Forest National Park, Mount Day	11.767° N, 42.650° E	BMNH 69.1256	F	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 41.31316	F	44	KJ509971	KJ509979	X	-	-
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 42.31317	F	45	KJ509972	KJ509980	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 43.31318	F	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 45.31369	F	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 49.33964	F	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 50.33965	F	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 56.36213	F	40	KJ509967	KJ509975	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 57.36214	F	41	KJ509968	KJ5009976	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 61.36218	F	43	KJ509970	KJ509978	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 63.36220	F	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	**NMP 91201**	F	39	EF216435	EF216467	-	-	-
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	**NMP 91201_B**	?	39	EF216436	EF216468	-	-	-
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	**NMP 91202**	F	38	EF216433	EF216465	-	-	-
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	**NMP 91202_B**	?	38	EF216434	EF216466	-	-	-
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	**NMP 91203**	F	36	EF216429	EF216461	-	-	-
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	**NMP 91203_B**	?	36	EF216430	EF216462	-	-	-
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	**PB 2512**	F	37	EF216431	EF216463	-	-	-
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	**PB 2512_B***	?	37	EF216432	EF216464	-	-	-
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 40.31315	M	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 44.31328	M	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 46.31370	M	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 47.31371	M	46	KJ509973	KJ509981	X	X	X

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 48.31372	M	-	-	-	X	X	X
Otomops harrisoni **sp. nov**. holotype	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 60.36217	M	42	KJ509969	KJ5009977	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	HZM 64.36220	M	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	SMF 41832	M	-	-	-	X	X	X
-''-	Ethiopia	Bale District, Sof Omar Cave	6.900° N, 40.859° E	SMF 41833	M	-	-	-	X	X	-
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 48654	F	-	-	-	X	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 63772	F	-	-	-	X	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 63779	F	-	-	-	X	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 63782	F	-	-	-	X	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 48655	M	-	-	-	X	-	-
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 48656	M	-	-	-	X	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 48660	M	-	-	-	-	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 48661	M	-	-	-	X	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 48663	M	-	-	-	-	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 48664	M	-	-	-	X	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 48666	M	-	-	-	X	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 48667	M	-	-	-	X	X	X
-''-	Kenya	19 km W of Makindu	2.300° S, 37.667° E	ROM 63808	M	-	-	-	X	X	X
-''-	Kenya	Chyulu Hills	2.350° S, 37.500° E	MRAC 38546	F	-	-	-	X	X	X
-''-	Kenya	Chyulu Hills	2.350° S, 37.500° E	MRAC 38547	F	-	-	-	X	X	X
-''-	Kenya	Chyulu Hills	2.350° S, 37.500° E	SMNS 46077	F	-	-	-	X	-	-
-''-	Kenya	Chyulu Hills	2.350° S, 37.500° E	SMNS 46079	F	-	-	-	X	-	-
-''-	Kenya	Chyulu Hills	2.350° S, 37.500° E	MRAC 38548	M	-	-	-	X	-	-
-''-	Kenya	Chyulu Hills	2.350° S, 37.500° E	MRAC 38549	M	-	-	-	X	X	X
-''-	Kenya	Ithundu Caves, Chyulu Hills, Makeuna District	2.358° S, 37.717° E	**NMK 15462** *	M	47	EF216428	EF216455	-	-	-
-''-	Kenya	Ithundu Caves, Chyulu Hills, Makeuna District	2.358° S, 37.717° E	NMK 15464	F	48	EF216439	EF216456	-	-	-
-''-	Kenya	Ithundu Caves, Chyulu Hills, Makeuna District	2.358° S, 37.717° E	**NMK 15460**	F	51	EF216442	EF216460	-	-	-

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	Kenya	Ithundu Caves, Chyulu Hills, Makeuna District	2.358° S, 37.717° E	**NMK 15463**	M	49	EF216440	EF216457	-	-	-
-''-	Kenya	Ithundu Caves, Chyulu Hills, Makeuna District	2.358° S, 37.717° E	**NMK 15459**	M	50	EF216441	EF216458	-	-	-
-''-	Kenya	Ithundu Caves, Kiboko	2.199° S, 37.717° E	ROM 65875	F	-	-	-	X	X	X
-''-	Kenya	Ithundu Caves, Kiboko	2.199° S, 37.717° E	ROM 65878	F	-	-	-	-	X	X
-''-	Kenya	Ithundu Caves, Kiboko	2.199° S, 37.717° E	ROM 65879	F	-	-	-	X	X	X
-''-	Kenya	Ithundu Caves, Kiboko	2.199° S, 37.717° E	ROM 65876	M	-	-	-	X	X	X
-''-	Kenya	Ithundu Caves, Kiboko	2.199° S, 37.717° E	ROM 65877	M	-	-	-	X	X	X
-''-	Kenya	Ithundu Caves, Makindu	2.333° S, 37.699° E	ROM 81198	M	-	-	-	X	X	X
-''-	Kenya	Ithundu Caves, Makindu	2.333° S, 37.699° E	ROM 81199	M	-	-	-	X	X	-
-''-	Kenya	Lake Baringo, Kampi Ya Moto	0.183° N, 35.867° E	ROM 68360	F	-	-	-	X	X	X
-''-	Kenya	Lake Baringo, Kampi Ya Moto	0.183° N, 35.867° E	ROM 68362	F	-	-	-	X	X	X
-''-	Kenya	Lake Baringo, Kampi Ya Moto	0.183° N, 35.867° E	ROM 68364	F	-	-	-	X	X	X
-''-	Kenya	Lake Baringo, Kampi Ya Moto	0.183° N, 35.867° E	ROM 68366	F	-	-	-	X	X	X
-''-	Kenya	Machakos District	1.517° S, 37.267° E	MRAC 35264	F	-	-	-	X	X	X
-''-	Kenya	Makindu Cave, Makindu	2.300° S, 37.833° E	ROM 78156	F	-	-	-	-	X	X
-''-	Kenya	Makindu Cave, Makindu	2.300° S, 37.833° E	ROM 78155	M	-	-	-	X	X	-
-''-	Kenya	Makindu Cave, Makindu	2.300° S, 37.833° E	ROM 78157	M	-	-	-	X	X	X
-''-	Kenya	Makindu Cave, Makindu	2.300° S, 37.833° E	ROM 78158	M	-	-	-	X	X	X
-''-	Kenya	Makindu River	-	ROM 65871	F	-	-	-	X	X	X
-''-	Kenya	Makindu River	-	ROM 65872	F	-	-	-	X	X	X
-''-	Kenya	Makindu River	-	ROM 65873	F	-	-	-	X	X	X
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	MNHN 1966-186	F	-	-	-	X		-
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 41920	F	-	-	-	X	X	-
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 41924	F	-	-	-	X	X	X
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 41927	F	-	-	-	X	X	-
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 41928	F	-	-	-	X	X	X

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 41932	F	-	-	-	-	X	X
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 78147	F	-	-	-	X	X	X
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 78148	F	-	-	-	X	X	X
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 78154	F	-	-	-	X	X	-
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	MNHN 1966-185	M	-	-	-	X		-
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 36517	M	-	-	-	X	X	X
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 36519	M	-	-	-	-	-	X
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 78151	M	-	-	-	X	X	-
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 78152	M	-	-	-	X	X	X
-''-	Ke*n*ya	Mount Suswa	1.150° S, 36.350° E	ROM 91249	M	-	-	-	X	X	X
-''-	Kenya	Mount Suswa	1.150° S, 36.350° E	ROM 91250	M	-	-	-	X	X	X
-''-	Kenya	Nairobi	1.280° S, 36.817° E	ROM 79677	F	-	-	-	X	X	X
-''-	Kenya	Near Makindu, 192 km E of Nairobi	2.300° S, 37.833° E	ROM 48657	M	-	-	-	X	X	-
-''-	Kenya	Near Makindu, 192 km E of Nairobi	2.300° S, 37.833° E	ROM 48659	M	-	-	-	X	X	X
-''-	Kenya	Near Makindu, 192 km E of Nairobi	2.300° S, 37.833° E	ROM 48662	M	-	-	-	X	X	X
-''-	Kenya	Near Kibwezi	-	HZM 12.11899	F	-	-	-	X	-	-
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	HZM 39.31195	F	-	-	-	X	X	X
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	HZM 52.33977	F	32	KJ509966	KJ509974	-	-	-
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	HZM 55.33980	F	-	-	-	X	X	X
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	SMF 87650	F	31	EF216437	EF216469	-	-	-
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	**NMP 91812**	F	34	KJ433730	KJ433789	-	-	-

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	**NMP 91814**	F	35	KJ433732	KJ433791	-	-	-
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	**NMP 91815**	F	33	KJ433733	KJ433792	-	-	-
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	**NMP 91816**	F	33	KJ433734	KJ433793	-	-	-
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	HZM 51.33976	M	-	-	-	X	X	X
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	HZM 53.33978	M	-	-	-	X	X	X
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	HZM 54.33979	M	-	-	-	X	X	X
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	**NMP 91811**	M	33	KJ433729	KJ433788	-	-	-
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	**NMP 91813**	M	33	KJ433731	KJ433790	-	-	-
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	SMF 87648	M	-	-	-	X	X	X
-''-	Yemen	Hud Sawa Cave, Ar-Rayadi Al-Gharbi Mountains, 3 km NW of Al-Mahweet	15.483° N, 43.533° E	SMF 87649	M	-	-	-	X	X	-
Otomops martiensseni s.s	Burundi	2.3 km N, 0.7 km W Teza, Kibira	3.200° S, 29.550° E	FMNH 137633	M	52	EF216423	EF216443	X	X	-
-''-	Central African Republic	Bamingui-Bangoran National Park	7.550° N, 19.290° E	BMNH 81.238	M	-	-	-	X	X	X
-''-	Ivory Coast	Comoé National Park	8.715° S, 3797° W	SMF 92048	M	-	-	-	X	X	X
-''-	Ivory Coast	Comoé National Park	8.715° S, 3797° W	SMF 92049	M	30	EF216420	EF216454	X	X	-
-''-	Ivory Coast	Comoé National Park	8.715° S, 3797° W	SMF 92050	F	-	-	-	X	X	X
-''-	Democratic Republic of Congo	Lufuko Stream, Marungu	7.400° S, 29.460° E	NZM 3395	M	-	-	-	X	X	X

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	Democratic Republic of Congo	Welle River, Poko	3.080° N, 25.580° E	BMNH 19.3.92	F	-	-	-	X	X	X
-''-	Malawi	Mangoche Mountain	14.450° S, 35.483° E	NZM 3228	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Berea, 26 Waller Crescent	29.825° S, 31.002° E	DM4760	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Berea, Hime Road	29.800° S, 31°010' E	DM 4950	M	-	-	-	-	X	X
-''-	South Africa	KwaZulu-Natal, Bluff	-	TM 33867	F	-	-	-	X	-	-
-''-	South Africa	KwaZulu-Natal, Bluff	-	TM 38865	F	-	-	-	X	-	-
-''-	South Africa	KwaZulu-Natal, Bluff	-	TM 42514	F	-	-	-	X	-	-
-''-	South Africa	KwaZulu-Natal, Bluff, 296 Marine Drive	29.916° S, 31.024° E	DM 5425	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Bluff, 296 Marine Drive	29.916° S, 31.024° E	DM 5426	F	-	-	-	-	X	X
-''-	South Africa	KwaZulu-Natal, Bluff, 560 Marine Drive	29.917° S, 31.007° E	DM 5514	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Bluff, 560 Marine Drive	29.917° S, 31.007° E	DM 5516	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Bluff, 560 Marine Drive	29.917° S, 31.007° E	DM 5518	F	-	-	-	X	-	X
-''-	South Africa	KwaZulu-Natal, Bluff, 560 Marine Drive	29.917° S, 31.007° E	DM 5509	M	-	-	-	-	X	X
-''-	South Africa	KwaZulu-Natal, Bluff, 560 Marine Drive	29.917° S, 31.007° E	DM 5511	M	-	-	-	-	X	X
-''-	South Africa	KwaZulu-Natal, Bluff, 560 Marine Drive	29.917° S, 31.007° E	DM 5512	M	-	-	-	-	X	-
-''-	South Africa	KwaZulu-Natal, Brighton Beach, 137 Glenardle Road	29.934° S, 30.003° E	DM 6930	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Bluff, 296 Marine Drive	29.916° S, 31.024° E	DM 5427	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Carrington Heights, Marshall Grove	29.883° S, 30.967° E	DM 3518	F	-	-	-	-	X	X
-''-	South Africa	KwaZulu-Natal, Central Durban	29.850° S, 31.017° E	BMNH 16.10.9.1	M	-	-	-	-	X	X
-''-	South Africa	KwaZulu-Natal, Doonheights, 2 Mopani Road	30.065° S, 30.865° E	N/A	F	28	KJ433726	KJ433785	-	-	-
-''-	South Africa	KwaZulu-Natal, Doonheights, 2 Mopani Road	30.065° S, 30.865° E	N/A	M	28	KJ433727	KJ433786	-	-	-
-''-	South Africa	KwaZulu-Natal, Durban	-	DM 5936	F	-	-	-	-	X	X

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	South Africa	KwaZulu-Natal, Durban	-	NM 379	F	-	-	-	-	X	X
-''-	South Africa	KwaZulu-Natal, Durban	-	DM 5392	M	-	-	-	X	-	-
-''-	South Africa	KwaZulu-Natal, Durban	-	DM 5936	M	-	-	-	-	X	-
-''-	South Africa	KwaZulu-Natal, Durban	-	DM 6904	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Durban	-	N/A	M	27	KJ433725	KJ433784	-	-	-
-''-	South Africa	KwaZulu-Natal, Morningside, Brynderyn Flats	29.864° S, 31.040° E	DM 7909	M	1	EF216424	EF21644	X	X	X
-''-	South Africa	KwaZulu-Natal, Durban	-	NM 378	M	-	-	-	-	X	X
-''-	South Africa	KwaZulu-Natal, Durban North	-	DM 11731	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Durban North, 229 Rinaldo Road	29.758° S, 31.044° E	DBN 18	M	12	KJ433700	KJ433759	-	-	-
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	DM 11434	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	**DBN 19**	F	14	KJ433701	KJ433760	-	-	-
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	**DBN 20**	F	21	KJ433702	KJ433761	-	-	-
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	**DBN 21**	M	22	KJ433703	KJ433762	-	-	-
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	**DBN 22**	F	14	KJ433704	KJ433763	-	-	-
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	**DBN 23**	F	23	KJ433705	KJ433764	-	-	-
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	**DBN 24**	F	16	KJ433706	KJ433765	-	-	-
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	**DBN 25**	F	12	KJ433707	KJ433766	-	-	-
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	**DBN 26**	F	9	KJ433708	KJ433767	-	-	-
-''-	South Africa	KwaZulu-Natal, Glen Anil, 29 Glen Anil Street	29.752° S, 31.037° E	**DBN 27**	F	24	KJ433709	KJ433768	-	-	-
-''-	South Africa	KwaZulu-Natal, Kloof, 99 Abelia Road	29.787° S, 30.839° E	DBN 15	F	12	KJ433697	KJ433756	-	-	-
-''-	South Africa	KwaZulu-Natal, Kloof, 99 Abelia Road	29.787° S, 30.839° E	DBN 17	F	9	KJ433699	KJ433758	-	-	-
-''-	South Africa	KwaZulu-Natal, Kloof, 99 Abelia Road	29.787° S, 30.839° E	DBN 16	M	15	KJ433698	KJ433757	-	-	-

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	South Africa	KwaZulu-Natal, Gillits, 6 Firwood Road	29.796° S, 30.808° E	**DBN 09**	F	16	KJ433691	KJ433750	-	-	-
-''-	South Africa	KwaZulu-Natal, Gillits, 6 Firwood Road	29.796° S, 30.808° E	**DBN 11**	F	18	KJ433693	KJ433752	-	-	-
-''-	South Africa	KwaZulu-Natal, Gillits, 6 Firwood Road	29.796° S, 30.808° E	**DBN 13**	F	20	KJ433695	KJ433754	-	-	-
-''-	South Africa	KwaZulu-Natal, Gillits, 6 Firwood Road	29.796° S, 30.808° E	**DBN 14**	F	12	KJ433696	KJ433755	-	-	-
-''-	South Africa	KwaZulu-Natal, Gillits, 6 Firwood Road	29.796° S, 30.808° E	**DBN 10**	M	17	KJ433692	KJ433751	-	-	-
-''-	South Africa	KwaZulu-Natal, Gillits, 6 Firwood Road	29.796° S, 30.808° E	**DBN 12**	M	19	KJ433694	KJ433753	-	-	-
-''-	South Africa	KwaZulu-Natal, Hillary	-	DM 5935	M	-	-	-	-	X	-
-''-	South Africa	KwaZulu-Natal, Kingsway, Kingsway School	30.039° S, 30.894° E	DM 7914	M	2	EF216425	EF216445	X	X	X
-''-	South Africa	KwaZulu-Natal, La Lucia	-	DM 6936	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, La Lucia	-	DM 6937	F	-	-	-	X	-	X
-''-	South Africa	KwaZulu-Natal, Morningside, Percy Osbourne Road	29.817° S, 31.017° E	DM 11732	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Northdene, 20 Jan Smuts Avenue	-	DM 3886	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Northdene, 20 Jan Smuts Avenue	-	DM 3885	M	-	-	-	-	X	-
-''-	South Africa	KwaZulu-Natal, Pinetown, 8 Buys Road	29.757° S, 30.639° E	**DM 8421**	F	7	EF216413	EF216447	X	-	X
-''-	South Africa	KwaZulu-Natal, Pinetown, 8 Buys Road	29.757° S, 30.639° E	**DP 2**	F	8	EF216415	EF216448	-	-	-
-''-	South Africa	KwaZulu-Natal, Pinetown, 8 Buys Road	29.757° S, 30.639° E	**DP 3**	F	8	EF216415	EF216449	-	-	-
-''-	South Africa	KwaZulu-Natal, Pinetown, 8 Buys Road	29.757° S, 30.639° E	**DP 4**	F	9	EF216416	EF216450	-	-	-
-''-	South Africa	KwaZulu-Natal, Pinetown, 8 Buys Road	29.757° S, 30.639° E	**DP 5**	M	-	-	-	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 106 Bailey Road	29.771° S, 31.023° E	DM 6886	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Red Hill, 106 Bailey Road	29.771° S, 31.023° E	DM 6887	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Red Hill, 106 Bailey Road	29.771° S, 31.023° E	DM 6888	M	-	-	-	X	X	X

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 28**	F	24	KJ433710	KJ433769	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 29**	F	16	KJ433711	KJ433772	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 30**	F	12	KJ433712	KJ433771	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 33**	F	12	KJ433715	KJ433774	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 34**	F	24	KJ433716	KJ433775	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 35**	F	16	KJ433717	KJ433776	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 36**	F	12	KJ433718	KJ433777	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 31**	M	16	KJ433713	KJ33772	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 32**	M	9	KJ433714	KJ433773	-	-	-
-''-	South Africa	KwaZulu-Natal, Red Hill, 10 Rosary Road	29.789° S, 31.017° E	**DBN 37**	M	16	KJ433719	KJ433778	-	-	-
-''-	South Africa	KwaZulu-Natal, Silverglen, 473 Silverglen Drive	29.928° S, 30.903° E	N/A	?	4	EF216407	EF216451	-	-	-
-''-	South Africa	KwaZulu-Natal, Silverglen, 473 Silverglen Drive	29.928° S, 30.903° E	N/A	?	5	EF216409	EF216452	-	-	-
-''-	South Africa	KwaZulu-Natal, Silverglen, 473 Silverglen Drive	29.928° S, 30.903° E	N/A	?	6	EF216410	EF216453	-	-	-
-''-	South Africa	KwaZulu-Natal, St Winifred, 50 Winifred Drive	30.089° S, 30.851° E	DM 6220	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Umbilo, Fenniscowles Road	29.883° S, 30.967° E	DM 5344	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	**DM 10294**	M	15	KJ433689	KJ433748	X	X	X
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	DM 8419	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	DM 8420	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	**DM 10295**	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	**DBN 01**	F	10	KJ433684	KJ433743	-	-	-
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	**DBN 02**	F	11	KJ433685	KJ433744	-	-	-

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	**DBN 03**	F	12	KJ433686	KJ433745	-	-	-
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	**DBN 04**	F	13	KJ433687	KJ433746	-	-	-
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	**DBN 05**	F	14	KJ433688	KJ433747	-	-	-
-''-	South Africa	KwaZulu-Natal, Umgeni Heights, 27 Hunters Way	29.808° S, 31.025° E	**DBN 08**	F	12	KJ433690	KJ433749	-	-	-
-''-	South Africa	KwaZulu-Natal, Umhlanga, Westbrooke	-	DM 4490	F	-	-	-	-	-	X
-''-	South Africa	KwaZulu-Natal, Wentworth	-	HZM 1.2145	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Wentworth	-	HZM 1.2145	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Westville, 5 Springfield Drive	29.833° S, 30.933° E	DM 8571	M	-	-	-	-	X	X
-''-	South Africa	KwaZulu-Natal, Winkelspruit, Eden Sands	30.099° S, 30.859° E	**KZN 01**	F	12	KJ433720	KJ433779	-	-	-
-''-	South Africa	KwaZulu-Natal, Winkelspruit, Eden Sands	30.099° S, 30.859° E	**KZN 02**	F	13	KJ433721	KJ433780	-	-	-
-''-	South Africa	KwaZulu-Natal, Winkelspruit, Eden Sands	30.099° S, 30.859° E	**KZN 03**	F	25	KJ433722	KJ433781	-	-	-
-''-	South Africa	KwaZulu-Natal, Winkelspruit, Eden Sands	30.099° S, 30.859° E	**KZN 04**	F	26	KJ433723	KJ433782	-	-	-
-''-	South Africa	KwaZulu-Natal, Winkelspruit, Eden Sands	30.099° S, 30.859° E	**KZN 05**	M	25	KJ433724	KJ433783	-	-	-
-''-	South Africa	Ugu District, Park Rynie	30.317° S, 30.733° E	DM 5605	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Voortukker Strand, near Margate, Durban	30.850° S, 30.367° E	HZM 3.3077	F	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Voortukker Strand, near Margate, Durban	30.850° S, 30.367° E	HZM 4.3078	F	-	-	-	X	X	-
-''-	South Africa	KwaZulu-Natal, Park Rynie, Ocean View Farm	30.339° S, 30.731° E	DM 8031*	F	3	EF216426	EF216446	X	X	X
-''-	South Africa	KwaZulu-Natal, Park Rynie, Ocean View Farm	30.339° S, 30.731° E	DM 8032	M	-	-	-	X	X	X
-''-	South Africa	KwaZulu-Natal, Pietermaritzburg, Queen Elizabeth Park	29.573° S, 30.326° E	DM 10790	M	-	-	-	X	X	X
-''-	South Africa	Limpopo, 3 km of Modimolle (Nylstroom)	24.660° S, 28.130° E	DM 11526	F	29	KJ433728	KJ433787	X	X	X

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
Otomops martiensseni s.s. holotype	Tanzania	Magrotto Plantation, Magrotto Hill, near Tanga	5.070° S, 38.030° E	MNHU 97523	M	-	-	-	X	X	X
-''-	Tanzania	Tongwe F.R., Tanga, Muheza District	5.306° S, 38.728° E	SMF 79542	M	54	EF216422	-	X	X	X
-''-	Uganda	Budongo Forest, Bunyoro	1.450° S, 31.350° E	ROM 46695	F	-	-	-	X	X	X
-''-	Zambia	Mafinga Mountains	10.250° S, 33.500° E	Unaccessioned specimen	M	-	-	-	X	X	X
-''-	Zimbabwe	Hostes Nicolle Institute, Sengwa Wildlife Ranch	18.167° S, 28.217° E	ROM 83979	M	53	EF216421	-	X	X	X
Otomops madagascariensis	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Analamerana, Grotte de Barazibe	12.711° S, 49.473° E	FMNH 178849	F	-	-	-	X	X	X
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Analamerana, Grotte de Barazibe	12.711° S, 49.473° E	FMNH 178850	F	-	-	-	X	X	X
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Analamerana, Grotte de Barazibe	12.711° S, 49.473° E	FMNH 178851	F	-	-	-	X	X	X
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Analamerana, Grotte de Barazibe	12.711° S, 49.473° E	FMNH 178852	M	-	-	-	X	X	X
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Ankarana, 3.5 KM se Andrafiabe	12.942° S, 49.055° E	FMNH 176355	M	-	-	-	X	X	X
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Ankarana, 3.5 KM se Andrafiabe	12.942° S, 49.055° E	FMNH 176356*	M	-	-	-	-	X	-
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Ankarana, 3.5 KM se Andrafiabe	12.942° S, 49.055° E	FMNH 176354	M	64	EF216381	EF216397	-	-	-
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Ankarana, 3.5 KM se Andrafiabe	12.942° S, 49.055° E	FMNH 176357*	M	65	EF216382	EF216400	X	X	-

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Ankarana, 3.5 KM se Andrafiabe	12.942° S, 49.055° E	FMNH 176376	M				X	X	X
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Ankarana, Grotte Antsiroandoha	12.891° S, 49.098° E	FMNH 177398	F	-	-	-	X	X	X
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Ankarana, Grotte Boribe	13.000° S, 49.000° E	FMNH 183896	F	-	-	-	X	X	X
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Ankarana, Grotte Boribe	13.000° S, 49.000° E	FMNH 183897	F	-	-	-	X	X	X
-''-	Madagascar	Province d'Antsiranana, Réserve Spéciale d'Ankarana, Grotte Boribe	13.000° S, 49.000° E	FMNH 183927	F	-	-	-	X	X	X
-''-	Madagascar	Province de Fianarantsoa, 3.8 km NW, Ranohira, along Namaza River	22.540° S, 45.380° E	FMNH 166073	F	55	EF216372	EF216383	X	X	X
-''-	Madagascar	Province de Mahajanga, Grotte d'Anjohibe, 3.7 km NE Antanamarina	15.537° S, 46.886° E	FMNH 179316	F	-	-	-	X	X	X
-''-	Madagascar	Province de Mahajanga, Grotte d'Anjohibe, 3.7 km NE Antanamarina	15.537° S, 46.886° E	FMNH 179317	F	-	-	-	X	X	X
-''-	Madagascar	Province de Mahajanga, Grotte d'Anjohibe, 3.7 km NE Antanamarina	15.537° S, 46.886° E	FMNH 179318	F	-	-	-	X	X	X
-''-	Madagascar	Province de Mahajanga, Parc National de Bemahara, Grotte d'Anjohimbabazimba	18.245° S, 44.716° E	FMNH 169689	F	-	-	-	X	X	X
-''-	Madagascar	Province de Mahajanga, Parc National de Bemahara, Grotte d'Anjohimbabazimba	18.245° S, 44.716° E	FMNH 169693	F	-	-	-	X	X	X
-''-	Madagascar	Province de Mahajanga, Parc National de Bemahara, Grotte d'Anjohimbabazimba	18.245° S, 44.716° E	FMNH 169667	M	56	EF216373	EF216384	-	X	X
-''-	Madagascar	Province de Mahajanga, Parc National de Bemahara, Grotte d'Anjohimbabazimba	18.245° S, 44.716° E	FMNH 169692	M	-	-	-	X	X	X

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	Madagascar	Province de Mahajanga, Parc National de Bemahara, Grotte d'Anjohimbabazimba	18.245° S, 44.716° E	FMNH 169694	M	57	EF216374	EF216385	-	-	-
-''-	Madagascar	Province de Mahajanga, Parc National de Bemahara, Grotte d'Anjohimbabazimba	18.245° S, 44.716° E	FMNH 169695	M	58	EF216375	EF216386	-	-	-
Otomops madagascariensis holotype	Madagascar	Province de Mahajanga, Réserve south of Province de Mahanja, Namoroka, Réserve naturelle intégrale no. 8	16.230° S, 45.280° E	MNHN.CG 1953-1	F	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte d'Ambanilia, 3.7 km SSE Sarodrano	23.540° S, 43.767° E	FMNH 172397	M	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte d'Ambanilia, 3.7 km SSE Sarodrano	23.540° S, 43.767° E	FMNH 172934	M	61	EF216378	EF216389	X	X	X
-''-	Madagascar	Province de Toliara, Grotte d'Ambanilia, 3.7 km SSE Sarodrano	23.540° S, 43.767° E	FMNH 172936	M	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte d'Ambanilia, 3.7 km SSE Sarodrano	23.540° S, 43.767° E	FMNH 172938	M	59	EF216376	EF216387	X	X	X
-''-	Madagascar	Province de Toliara, Grotte d'Ambanilia, 3.7 km SSE Sarodrano	23.540° S, 43.767° E	FMNH 172939	M	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte d'Ambanilia, 3.7 km SSE Sarodrano	23.540° S, 43.767° E	FMNH 172940	M	60	EF216377	EF216388	X	X	X
-''-	Madagascar	Province de Toliara, Grotte d'Ambanilia, 3.7 km SSE Sarodrano	23.540° S, 43.767° E	FMNH 172942	M	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172949	F	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte d'Ambanilia, 3.7 km SSE Sarodrano	23.540° S, 43.767° E	FMNH 172941	M	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172943	F	-	-	-	X	X	X

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172944	F	62	EF216379	EF216390	X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172945	F	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172949	F	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172952	F	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172953	F	-			X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	**SMG 16453**	F	66	KJ433735	KJ433794	-	-	-
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	**SMG 16454**	F	67	KJ433736	KJ433795	-	-	-
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	**SMG 16456**	F	69	KJ433738	KJ433797	-	-	-
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	**SMG 16459**	F	71	KJ433741	KJ433800	-	-	-
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172947	M	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172948	M	63	EF216380	EF216391	X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172950	M	-	-	-	X	X	X
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	FMNH 172951	M	-	-	-	X	-	-
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	**SMG 16455**	M	68	KJ433737	KJ433796	-	-	-

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	**SMG 16457**	M	62	KJ433739	KJ433798	-	-	-
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	**SMG 16458**	M	70	KJ433740	KJ433799	-	-	-
-''-	Madagascar	Province de Toliara, Grotte de Bishiko, 0.75 km E of St Augustin	23.548° S, 43.716° E	**SMG 16460**	M	71	KJ433742	KJ433801	-	-	-
Otomops wroughtoni	Cambodia	Preah Vihear Province, Chhep District	13.893° N, 105.267° E	HZM 3.33440	M	72	EF504251	EF504253	-	X	X
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	BMNH 13.4.9.1	M	-	-	-	X	X	X
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	BMNH 13.4.9.2	M	-	-	-	-	X	X
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	BMNH 13.4.9.3	M	-	-	-	X	-	-
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	BMNH 13.4.9.4	M	-	-	-	-	X	X
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	HZM 2.5005	M	-	-	-	-	X	X
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	BMNH 12.11.24.1	F	-	-	-	X	X	X
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	BMNH 13.4.9.5	F	-	-	-	X	X	X
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	BMNH 13.4.9.6	F	-	-	-	X	X	X
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	HZM 1.25004	F	-	-	-	-	X	-
-''-	India	Karnataka, 0.5 km from Talewadi Village, Barapede Caves	15.417° N, 74.367° E	MNHN 1985-1590	F	-	-	-	X	X	X

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APPENDIX 1. (Continued)

Species	Country	Locality	Coordinates	Museum No.	Sex	Haplotype No.	Cyt *b*	D-loop	Traditional Morphometrics	Geometric Morphometrics (dorsal)	Geometric Morphometrics (ventral)
Otomops secundus	New Guinea	Tapu, Upper Ramu River Plateau	-	BMNH 50.982	M	-	-	-	X	X	X
-''-	New Guinea	Tapu, Upper Ramu River Plateau	-	BMNH 50.979	F	-	-	-	X	X	X
-''-	New Guinea	Tapu, Upper Ramu River Plateau	-	BMNH 50.980	F	-	-	-	X	X	X
Otomops cf. *formosus*	Philippines	Luzon Island, Kalinga Province, Balbalan Municipality, Balbalasang Brgy, Magdallao	17.458° S, 121.068° E	FMNH 167240	M	73	EF504252	EF504254	X	X	X
-''-	Philippines	Mindanoa Island, Bukidnon Province, Sumilao Municipality, 10.6 km S, 2.8 km W Sumilao	8.189° S, 124.92°2 E	FMNH 167382	M	-	-	-	X	X	X
Otomops papuensis	Papua New Guinea	Milne Bay Province, Mount Suckling, Maul	-	BMNH 73.136	M	-	-	-	X	X	X
Mops midas	Madagascar	Antanimbary	-	FMNH 185120	M	74	EF474039	EF474062	-	-	-
Mops leucostigma	Madagascar	Ambondramamy	16.436° S, 47.156° E	FMNH 184701	M	75	EF474029	EF474076	-	-	-
-''-	Madagascar	Mahajanga	15.708° S, 46.312° E	FMNH 184698*	?	-	-	-	-	-	-
Mops condylurus	South Africa	Phinda Private Game Reserve	27.871° S, 32.344° E	DM 6332*	M	-	-	-	-	-	-
Mormopterus francoismoutoui	Mascarene Islands, Reunion	Sainte Clotilde	20.918° S, 55.483° E	FMNH 194015*	M	-	-	-	-	-	-
Mormopterus jugularis	Madagascar	Ankazobe	18.314° S, 47.114° E	FMNH 184835*	M	-	-	-	-	-	-
Myotis goudoti	Madagascar	Befotaka	23.830° S, 46.970° E	FMNH178603	?	77	GU116768	GU116752	-	-	-
Pipistrellus abramus	Japan	not given in original paper	-	not given in original paper	?	76	NC_005436	NC_005436	-	-	-